FOREWORD

RESEARCH ON ANIMAL ECOLOGY AND ITS PUBLICATION.

THE increasing number of papers dealing with animals submitted to the Editor of *The Journal of Ecology* and for which there is no space, has brought into prominence the problem of finding means for their publication. At present such papers are published in a number of different British journals (as may be seen from the abstracts of these papers on animal ecology which have appeared in *The Journal of Ecology*). Their number is increasing, and will undoubtedly increase even more rapidly in the near future. It therefore appeared to the Council of the British Ecological Society that steps ought to be taken now to make adequate provision both for centralising to some extent the widely scattered papers on animal ecology that are now being produced, and also, by planning well ahead, to anticipate the future development of the subject, which runs a real risk of becoming split unnaturally into isolated compartments of knowledge attached to special scientific and economic spheres, and therefore of losing the advantages which come from the pooling of ideas and knowledge in a central journal.

RELATION TO ECONOMIC ECOLOGY.

What has been said applies more particularly to papers dealing with population problems in animals (census work, fluctuations in numbers, migration), animal behaviour and allied subjects. Authorities on economic entomology, marine fisheries, economic ornithology and mammalogy, who have been consulted on this matter, are unanimous in their agreement about the desirability of centralised publication for animal ecology. This fact is of importance since so much work on animal ecology is at present subsidised directly from economic sources and so forms the greater bulk of the material published.

A NEW JOURNAL.

Various practical difficulties prevent expansion of *The Journal of Ecology* to meet this situation. After careful consideration, therefore, the Council of the British Ecological Society have decided to launch in 1932 a new journal, under the control of the Council of the Society, but separately financed and edited, and to be called *The Journal of Animal Ecology*. This journal will publish primarily papers dealing exclusively with animals (such as population and migration studies and allied problems), and with methods of research having reference primarily to animals. On the other hand, comprehensive biological survey papers dealing with both plants and animals, papers on the nature of biotic communities, and such problems as effects of grazing on plant succession,

will appear as heretofore in *The Journal of Ecology*. With these exceptions, it is intended that the new journal shall act as the organ of research on animal ecology in the British Isles, while at the same time dovetailing with *The Journal of Ecology*, which will continue to be the forum for discussions of general ecological theory.

Contents of the new journal. It is proposed that *The Journal of Animal Ecology* should contain original papers on the subjects already indicated, also summary papers, abstracts, short notes and reviews. There will be two numbers each year. These will be published in May and November. The journal will be printed and distributed by the Cambridge University Press.

Editors. Mr Charles Elton is editor, and Mr A. D. Middleton, assistant editor.

Financial arrangements. The successful launching of this new journal depends on the active support received from Members of the Society and others interested in the development of animal ecology. Those unable to assist by subscribing can do a great deal to help by putting the Editors in touch with possible subscribers in all parts of the world, and by recommending the journal to libraries.

Subscriptions of members. The cost of the new journal to members of the British Ecological Society will be twenty-five shillings per annum (the cost of taking both this and *The Journal of Ecology* being forty-five shillings). Subscriptions are payable in advance, and should be sent to the Secretary of the British Ecological Society, Dr H. Godwin, Botany School, Cambridge.

Subscriptions of non-members. For non-members of the Society the subscription to *The Journal of Animal Ecology* is thirty shillings per annum payable in advance. No reduction is made if both journals are taken. These subscriptions should be sent direct or through an agent to The Cambridge University Press, Fetter Lane, E.C. 4.

Other communications (concerning contributions, suggestions, etc.), should be sent to The Editor, *Journal of Animal Ecology*, University Museum, Oxford.

THE ROOKERIES OF THE WIRRAL PENINSULA

By B. J. MARPLES, B.A.

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(*With one Map in the Text.*)

Introduction.

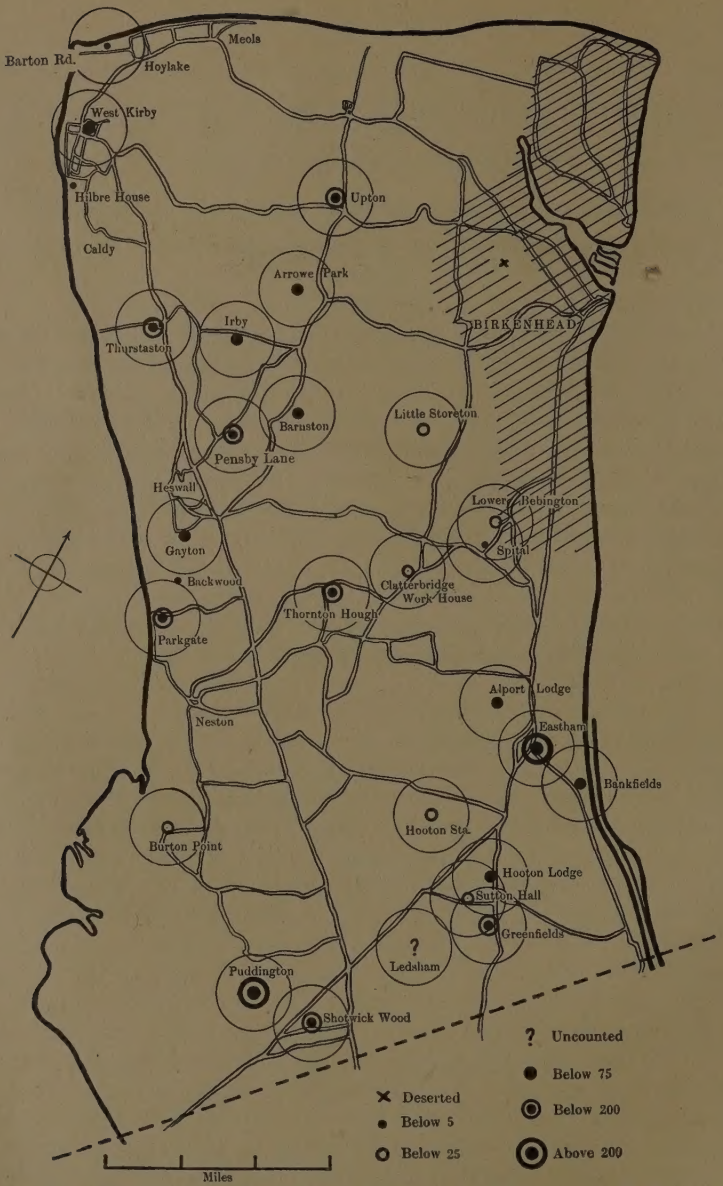
The rook has been selected by the Oxford Ornithological Society as a suitable bird for the study of its ecology and relations to agriculture. Its large size and habit of nesting in conspicuous colonies renders it particularly suitable for this kind of work, and there has been considerable discussion as to whether it is beneficial or injurious to crops. The Oxford Ornithological Society took a preliminary census of the rooks' nests in an area of 224 square miles round Oxford, and an account of this work has been published by the Nicholsons (**5**). There is a considerable variety of country round Oxford, hills, river flats, large woods, and a number of fairly large rivers, and it seemed desirable to carry out a rook census in a different type of country and to compare the results with those obtained near Oxford. The present paper deals with the rook population of an area of the Wirral Peninsula during the years 1928 and 1929.

Description of area.

The Wirral Peninsula is that part of the county of Cheshire lying between the estuaries of the rivers Mersey and Dee. It is about 18 miles long and roughly rectangular in shape, the width varying from about 6 to 8 miles. The long axis runs north-north-west by south-south-east. Strictly speaking the peninsula extends as far as a line joining the river Dee at Chester and the point where the river Weever enters the Mersey, but for the purpose of the present census only the area north of a line drawn between Ellesmere Port and Queensferry is considered. The area comprises about 90 square miles and is bounded on the east by the Mersey estuary, on the north by the sea coast and on the west by the Dee estuary. Birkenhead and the other towns confluent with it occupy about 9 square miles in the north-east corner of the peninsula.

The northern part of the peninsula consists of flat land fringed with sand-hills along the coast, but about a mile and a half inland the land rises gradually to the general level of the plateau, which is about 120–160 ft. high. Along each side of the plateau, parallel to the estuaries, run ridges of higher ground, gradually decreasing in height toward the southern end of the area. The highest point is only 359 ft., at Heswall about the middle of the western ridge, so the area, though undulating in parts, has no large hills.

The rocks are Triassic sandstones and marls, and these are only exposed along the tops of the ridges. The rest of the surface, except for a few small areas



Map of the Wirral Peninsula showing the position and size of the rookeries. To facilitate comparison the signs used to denote the size of the rookeries are the same as those used by the Nicholsons. Circles of half a mile radius are drawn round each rookery to indicate the hypothetical "nesting territory." Only the principal roads are shown, and the area covered by town is shaded. (Based upon the Ordnance Survey Map with the sanction of the Controller of H.M. Stationery Office.) (Cambridge University Press.)

round the coast of blown sand and alluvium, is covered with boulder clay. The streams of the area are small and mostly slow running. The drainage is chiefly into the Mersey, there being two stream systems, one in the north entering Wallasey Pool and one in the centre of the peninsula entering Bromborough Pool. There are a considerable number of trees particularly small oaks in the field hedges, and numerous small woods in which elm and ash predominate. In the flat district near the sea coast there are no woods and few trees except wind-blown willows. In the Petty Sessional Division of Wirral, which is roughly the same as the area under consideration, there were 31,605 acres under crops and grass in June, 1928 (see Table I).

Table I. *Acreage under crops and grass in the Petty Sessional Division of Wirral, June* 1928.

	Acres
Wheat...	573
Barley...	22
Oats	3,664
Mixed corn	89
Total cereals	4,348
Peas and beans	65
Potatoes	1,401
Roots	1,050
Other crops	679
Grass	24,062
Total crops and grass ...	31,605

RESULTS OF CENSUS.

The work of counting the nests and rookeries was carried out in April, 1928 and 1929. It is believed that all the rookeries were located, but unfortunately it was not possible to visit every one. In 1928 it was hoped that all the rookeries would be found so that a complete count could be made the following year, but in 1929, however, two of those visited the previous year were not counted, and one rookery, seen from the train, was not visited at all. These omissions are not very serious, as in each case the position of the rookery and its approximate size is known. The unvisited rookery, one near Ledsham, contained at least 30 nests in 1929, while of the other two important ones not counted that year, the Upton one appeared on superficial examination to have increased, and an outlying colony of 8 nests had been formed about 100 yards away.

Most of the rookeries are compact and in small isolated woods. The largest wood containing a rookery is in Arrowe Park, but the nests are all in one group, and the same is found in several places such as Shotwick Wood or Bankfields Wood near Eastham, where the nests are all at the end of long woods. In West Kirby, however, they are scattered, there being a main colony of 40 nests with small groups and odd nests distributed at varying distances from it. The nesting sites here seem to vary from year to year, and as this seems to be a recently formed rookery it is possible that it has not become stabilised yet. The rookery at Irby is situated in a long narrow wood and the nests are spread out more or

less evenly along its length. At Barnston, where the conditions are similar, the rookery is composed of two groups of 17 and 27 nests respectively about 100 yards apart, with one or two nests half-way between, while at Heswall there are 67 nests at one end of a long wood and 8 at the other. This supports the conclusions arrived at by the Nicholsons from the results of the Oxford census, that when the rookery is situated in a wood where there is room for expansion in all directions, it will continue to retain its unity although it may increase in size. When the nesting trees are spread out in a long line, such as the hedgerow elms near Oxford, the two ends of the colony will tend to become separated and form distinct colonies. That such straggling colonies are not common in Wirral is probably due to the absence of these lines of large trees. The scattered colonies mentioned above are each counted as one rookery in the list given in Table II.

The number of rookeries in the area was 28, having a total number of 1704 nests. The largest was at Puddington with 425 nests, and was nearly twice the size of the next largest, the one at Eastham which had 232 nests. The average number of nests per rookery was 63·1, there being 9 rookeries with a greater and 19 with a smaller number than the average. Table II gives a list of the rookeries in the order of size in 1929 with the number of nests for the two years.

Table II.

Rookery	1928	1929	Change
Puddington	—	425	—
Eastham	200	232	Up 32
Greenfields, nr. Little Sutton ...	130	134	Up 4
Thornton Hough...	69	82	Up 13
Thurstaston	16	80	Up 64
Upton	80	—	—
Shotwick Wood	—	77	—
Parkgate	—	76	—
Pensby Lane, Heswall	73	75	Up 2
West Kirby	47	58	Up 11
Arrowe Park	55	—	—
Irby	26	54	Up 28
Barnston	32	45	Up 13
Hooton Lodge, Childer Thornton	21	39	Up 18
Alport Lodge, nr. Eastham ...	—	38	—
Gayton	20	26	Up 6
Bankfields, nr. Eastham ...	27	26	Down 1
Burton Point	—	23	—
Clatterbridge Work House ...	28	23	Down 5
Lower Bebington	20	19	Down 1
Hooton Station	15	13	Down 2
Sutton Hall	13	13	Same
Little Storeton	5	—	—
Backwood, nr. Gayton	3	—	—
Spital	15	1	Down 14
Barton Road, Hoylake	0	1	Up 1
Hilbre House, West Kirby ...	1	1	Same
Ledsham	?	?	—

The nests in 18 rookeries were counted in both years and in 11 of these the numbers increased, in 5 they decreased and in 2 they remained the same. It is

possible that when the counts were made in 1928 the birds had not finished building, but as they were made about the same period each year, in late March and early April, it seems unlikely that there would be much difference because of this. The Thurstaston rookery is noteworthy as its numbers increased from 16 to 80 nests. This cannot have been due to immigration from neighbouring rookeries, as these also increased in size. The great decrease in the Spital rookery is due to the fact that most of the trees in which the colony was situated were cut down. In all other cases the decrease is only small. There seem to be considerable local variations in the numbers of rooks, and census work over a period of several years would provide some very interesting data.

There appears to be a tendency for rooks to build near houses, 18 out of the 28 rookeries being in the grounds of large houses or close to them. This is rather remarkable, as rook shooting is widespread, and the birds do not seem to feed upon the refuse from houses to any great extent. Out of 209 rooks' stomachs examined, Leigh (4) records only 9 containing substances of this kind.

The species of trees in which the nests were built was recorded for 1049 nests, and the percentage of nests for each species of tree is given in Table III. These numbers do not seem to indicate any particular preference, the species most often used being the commonest woodland trees in the area. The Puddington rookery, with 425 nests, was amongst those in which the species of trees containing nests was not noted. Most of the nests in this rookery were in ash trees, and therefore this species would have a higher percentage if the table included all the nests in the area. This also supports the Nicholsons' findings, that there seems to be no special preference for any species of tree, the ones used most often being the commonest.

Table III. *Percentage of* 1049 *nests found in the different species of trees.*

	%
Elm	44·4
Beech	29·3
Sycamore	13·6
Ash	8·2
Oak	2·4
Conifer	0·8
Birch	0·6
Chestnut	0·6
Holm Oak	0·1

DISTRIBUTION.

The rookeries were not evenly distributed over the whole of the area, there being two regions where none were found. One of these extended across the north end of the peninsula, and consisted of the flat land near the coast which is very much exposed to wind and has few trees. There was formerly a small colony of 6 or 7 nests in Barton Road, Hoylake, within a few yards of high-tide mark, this being the rookery nearest to the sea coast, though several were near to the estuaries. It was situated in the garden of a large house, on the side

sheltered from the prevailing wind, which may account for its position. The birds were frequently to be seen feeding on the shore along the tide mark. It was abandoned 5 or 6 years ago, but in 1929 it was again occupied, there being a single nest. The other unoccupied area was in the south-westerly part of the peninsula between the villages Thornton Hough, Hooton, Shotwick, Burton and Neston, and there is no obvious reason for the absence of nests. The apparent tendency for rookeries to be placed near houses may possibly have some bearing on this, as the villages here are more widely scattered than elsewhere. The largest rookery recorded lies on the edge of this unoccupied region, but to judge from the distribution of the others, the size of the rookery does not affect its distance from its neighbours.

Apart from these unoccupied areas there was a considerable tendency for the rookeries to be spaced out at distances of 1 mile from one another. The most isolated colony was at West Kirby, nearly 3 miles from the one at Thurstaston, but it had the impermanent colony at Barton Road, Hoylake 1 mile from it, and there was formerly a rookery at Caldy between West Kirby and Thurstaston. In very few cases was the distance between the rookeries much less than 1 mile. The Lower Bebington and Spital rookeries were only half a mile apart, but they were more in the town than any of the others and this may have caused abnormal conditions. The group of rookeries in and about Little Sutton were also within half a mile of one another. Probably the whole group should be classed as a single diffuse rookery similar to that found at West Kirby. Several short-distance movements are known to have occurred in the past at both places.

As has already been mentioned, the size of a rookery does not seem to affect its distance from adjoining colonies. The large Puddington rookery was just over a mile from the one in Shotwick Wood, though isolated on the other side, but the next largest, the one at Eastham, was unusually near to its two neighbours. Consequently it does not appear that this spacing out of colonies indicates any division of the country into feeding territories. The rook is an active bird and certainly forages for food much further than half a mile from the rookery. It is frequently seen at Meols, which is in the unoccupied area in the north over 2 miles from the nearest colony. No rookery in the area was so surrounded by others that the birds from it could not easily reach unoccupied country without going within half a mile of the neighbouring rookeries. It seems possible that the rooks keep this area as a nesting territory, and forage further afield in unoccupied country for food. Howard (**3**) has described similar behaviour in peewits. He found that several pairs which nested in the same field kept a small area round the nest as a breeding territory, while the feeding ground was further away and common to all the birds. The question might be decided by observations on the feeding areas of the rooks of neighbouring colonies, and their behaviour towards one another, but it was not possible to carry this out in connection with the present investigation. It is, of course,

impossible to draw any definite conclusions from the results found in so small an area, but the point is one of great interest. The Nicholsons state that the rookeries near Oxford are very far from occurring at regular intervals, but judging from their map there does seem to be a distinct tendency for adjacent colonies to be a mile apart. The Oxford area is much larger and more varied than the Wirral. It is therefore particularly interesting to find that though the general distribution of the rookeries is much more irregular, when they are near together they are spaced out much as they are in the Wirral. The same thing has been noticed in other districts also. Of 6 rookeries in the south of the Isle of Man for example, 4 are 1 mile from their nearest neighbours and the others about 2 miles. From the available evidence it seems that the usual minimum distance between rookeries is 1 mile, irrespective of the size of the colonies.

Though rookeries in a great many cases are occupied annually for many years, there are a considerable number of changes. In some cases the birds are deliberately driven away by the owners of the land. The colony existing at Caldy about 25 years ago is said to have been driven away by fixing a number of dead cats in the branches during the incubation period. The birds moved to Hilbre House, West Kirby, and in 1919 there were about 20 nests, but these gradually diminished till in 1929 there was only one. The rest of the birds appear to have moved into West Kirby, where the main colony is now situated. In 1930 there were 3 nests at Hilbre House. Possibly if the histories of all the rookeries were known it would be found that a great deal of this moving about takes place; past movements at Birkenhead Park, West Kirby, Caldy, Thingwall, Gayton and Little Sutton are known to have occurred. In some cases deserted sites are recolonised after an interval of several years, as at Barton Road, Hoylake, and Birkenhead Park, where the rookery was abandoned in 1921 after being occupied for years and again occupied in 1930. New colonies are sometimes formed, perhaps when the birds are driven away from their original nesting site, or gradually increase from a single nest. At Backwood this took place about 50 years ago and a flourishing colony developed. It was later disturbed by tree felling and only 3 nests remained in 1928. These examples show that fluctuations and movements of rookeries are fairly common, but unfortunately it is not possible to determine whether the rook population of the whole area has varied in the past. In the 18 rookeries whose nests were counted both in 1928 and 1929, there was a total increase of 171 nests in 1929. Rook shooting appears to be widely practised, but it does not as a rule seem to do more than keep the numbers in a colony fairly constant.

Mention must be made of other species of birds which may compete with the rooks in the search for food. Blackheaded gulls (*Larus ridibundus*) are plentiful and must be severe competitors especially in the plough land, but as there is no nesting colony in the peninsula they are mostly absent in the breeding season. Peewits (*Vanellus vanellus*) occur in large flocks in the winter, at times accompanied by numbers of golden plover (*Charadrius apricarius*),

and a good many of them nest in the area during the summer. The only other species which seems likely to be an important competitor of the rook is the starling (*Sturnus vulgaris*). These are common throughout the district, especially in winter when large flocks are to be seen, there being a very large roost just outside the southern boundary of the area. Jackdaws (*Corvus monedula*) are present in negligible numbers and wood pigeons (*Columba palumbus*) are scarce, especially in the northern half of the peninsula.

The average density of rooks' nests in the Wirral Peninsula, taking the area to be 90 square miles, was 18·9 nests per square mile. This is about the same as the density found in the least populated quadrant of the Oxford area, 48 square miles, where there were 15·33 nests per square mile. In the Wirral, allowance should be made for the large area covered by town. If this is taken as 9 square miles the density of the rook population for the whole area was 21·0 nests per square mile. According to Collinge (**1**) 35·1 per cent. of the food of the rook consists of cereals, 13·4 per cent. of potatoes and roots, and 28·5 per cent. of insects injurious to crops, so it is clearly the density of the rook population on the land where cereals and roots are grown which is of importance. In the Petty Sessional Division of Wirral there were, in June 1928, 6799 acres under cereals and roots (see Table I). If it is assumed that there were 3500 rooks in the area, allowing for a small percentage of non-breeding birds, there was therefore only 1 rook for every 1·9 acres under these crops, and the damage done can only have been very slight and probably easily counterbalanced by the number of injurious insects destroyed.

The density of rooks per acre of land under cereals was about the same in the Oxford area, roughly 1 bird for every 2 acres. As the Nicholsons point out, it is impossible to determine the entire effect of rooks upon agriculture until the food chains involved have been worked out, but the evidence seems to point to the fact that if these birds are injurious to agriculture at all this effect can only be very slight.

Summary.

1. A census was taken of the rookeries and rooks' nests in an area of about 90 square miles on the Wirral Peninsula, Cheshire.

2. This is a uniform area, and the results are compared with those obtained by the Oxford Ornithological Society's Census of Rookeries in an area of 224 square miles of diversified country round Oxford.

3. There is a distinct tendency for rookeries, when numerous, to be situated 1 mile apart, and though they are frequently more widely separated it is exceptional for them to be nearer together. It is suggested that this may be due to the presence of "nesting territories" near the rookery, while the feeding areas are farther afield. Observations on the habits of rooks are necessary to test this suggestion.

4. The number of rooks per acre of cereals, 0·51, is about the same as in the Oxford area. It seems probable that rooks are only slightly if at all harmful to agriculture.

ACKNOWLEDGMENTS.

In conclusion I wish to acknowledge my indebtedness to my father for facilities which rendered the actual census work possible, to the editors of the *Liverpool Post and Mercury* and the *North-western Naturalist* for kindly publishing letters asking for information about rookeries, and to all those correspondents who wrote to me in reply to those letters. For much useful information about the physical features I am indebted to W. Hewitt's book (**2**), and to the Statistical Branch of the Ministry of Agriculture and Fisheries for the details of the numbers of acres of land under various crops.

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STUDIES OF FLUCTUATIONS IN INSECT POPULATIONS

I. THE INFESTATION OF BROADBALK WHEAT BY THE WHEAT BLOSSOM MIDGES (CECIDOMYIDAE)

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(*With six Figures in the Text.*)

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I. Foreword.

The number of insects in any population varies from time to time on account of many factors, such as disease, lack of food, climatic conditions and the intervention of natural enemies and man. The fundamental and economic importance of any additional information regarding such fluctuations is very obvious, especially in the case of insects not easily controlled by the usual methods. For this reason, the gall midges (Cecidomyidae) are pre-eminently suitable for such a study, being also readily obtainable in large numbers.

There are several means of approaching the subject. One favourite method is to keep a population under controlled conditions, whether constant or fluctuating, in the laboratory and to determine the effects on the insects in question. Another method is to make field observations of a phenological type and then attempt to correlate noticed fluctuations with the factors involved. There are obvious weaknesses in employing either of these two methods by itself. Two such drawbacks may be mentioned. It is very easy to use con-

ditions in the laboratory that would not occur in a state of nature; and phenological observations depend too largely on the personal factor. The technique necessary to avoid the latter renders the method too extravagant in man-power for general use.

The method adopted by the author has been to take samples of wild populations in the fully fed larval stage and to rear, to the imaginal stage in an outdoor insectary, both the host insect and its parasites. Care has been taken to check results by plentiful observations in the field. Certain procedures, which are independent so far as is possible of the individual worker, have been followed, in order that the study could be put on a routine basis if necessary. In this way it would be possible for the study to be carried on over a longer period of years than if only one worker were involved.

This study of insect populations is designed primarily to collect information regarding periodic fluctuations as they occur in nature, and secondly to provide hints of the factors involved. It is intended to test out any warrantable hypotheses that may be drawn from this data by critically controlled experiments. Two such subsidiary studies have already appeared, viz. "Some factors governing the emergence of gall midges" (Barnes, 1930), and "The sex ratio at the time of emergence and the occurrence of unisexual families in gall midges" (Barnes, 1931). A third, "A study of the segmentation of the antennae in gall midges," is now in the press.

Three avenues of approach to the problem have been taken into consideration. They are firstly, the *degree of infestation* of the crop in question. The two wheat blossom midges, *Contarinia tritici* (Kirby) and *Sitodiplosis mosellana* (Géhin), and a midge, *Dasyneura alopecuri* (Reuter), which lives on the seed of meadow foxtail grass, are being used in this phase. Secondly, there is the *degree of parasitism*, which is being studied in these three species and also the button top midge of basket willows, namely *Rhabdophaga heterobi* (H. Lw.). Thirdly, the *dates of emergence and number of broods* are being taken into account in the case of the above four midges and, in addition, the leaf-curling pear midge, *Dasyneura pyri* (Bouché), and the Arabis midge, *Dasyneura arabis* Barnes. In each case the observations are intended to be carried out over an initial period of 5 years.

II. INTRODUCTION.

The present paper deals with the infestation of a classical experimental field of wheat (Broadbalk) by the wheat blossom midges over a period of 5 years. The variety of wheat on this field is Standard Red. Biological information concerning the midges is dealt with as well as the fluctuations in degree of infestation of the wheat by the midges. The two species, *Contarinia tritici* (Kirby) and *Sitodiplosis mosellana* (Géhin) may be regarded as single brooded, although sometimes there is a partial second emergence of adults in the case of *C. tritici*.

A sample of wheat ears was gathered each year about 3 weeks after the crest of emergence of the adults. In this way the sample was picked at the time when the maximum number of larvae were present in the ears. It consisted of 500 ears, fifty being gathered from each of ten plots, all of which have been under different manurial treatment over a large number of years. The ten plots were chosen with a view to determining whether differential manuring affected the incidence of attack. The whole sample gave, on examination, the degree of infestation at the time when it was taken.

In order to determine the date for sampling, the larvae obtained from the previous year were kept and reared in an outdoor insectary at as nearly normal outside conditions as possible. The dates of emergence so obtained were checked up with field observations concerning the time of oviposition. This is allowable, since the midges are very short lived and oviposit as a rule the same day as they emerge.

The rearing of this material gave, in addition, a figure for the degree of parasitism at the time of emergence of host and parasites. This figure is called that of *relative or effective parasitism*, since any figures obtained by examining the midge larvae would only give the parasitism of the larvae and not the relative number of parasites to host which would be on the wing the following summer. This is due to the fact that nearly 10 months elapse between the time the midge larvae are fully fed and the emergence of the adults, and to the probability that weather conditions act differentially on the parasites and host. The fluctuations in relative parasitism will be dealt with in more detail when additional information has been amassed.

III. Identification.

The two species are very easily distinguishable after a little practice. The main morphological and colour differences have already been noticed (Barnes, 1928). The adults, larvae and eggs of *C. tritici* are golden yellow, while the same stages of *S. mosellana* are orange to carrot-red. The accompanying diagrammatic figures (Figs. 1 and 2) indicate the chief morphological characters of the two species.

IV. Biology and distribution.

(*a*) *C. tritici*.

This species is on the wing from the time that normal flowering wheat ears first break their sheaths till about 5 weeks later, i.e. June to early July. Emergence takes place from pupae in the soil. The usual time of emergence is the evening. Hourly observations during the day have shown that 7 per cent. of the males and 10 per cent. of the females emerge between 9 a.m. (standard time) and 2 p.m., a further 30 per cent. of the males and 40 per cent. of the females appear between 2 p.m. and 8 p.m., and the remaining 63 per cent. of the males and 50 per cent. of the females emerge between 8 p.m. and 9 a.m.

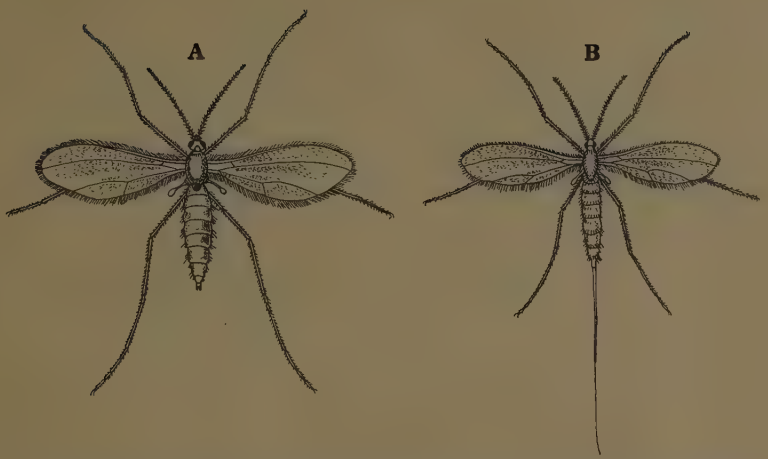

Fig. 1. Adult female midges: A, *Sitodiplosis mosellana* (Géhin); B, *Contarinia tritici* (Kirby). (After Wagner.) Reproduced by permission of the Imperial Institute of Entomology.

Fig. 2. Larvae of wheat blossom midges: A, anchor process of *Sitodiplosis mosellana*; B, anal extremity of *S. mosellana*; C, anchor process of *Contarinia tritici*; D, anal extremity of *C. tritici*. Reproduced by permission of the Imperial Institute of Entomology.

the following morning. The great bulk of these two last percentages emerges before 1 a.m.

As soon as emergence has taken place mating occurs and within a very few minutes the females are ovipositing on the ears. The males remain near the soil waiting for the females to emerge. The midges are short lived and their average life seems to be only a few hours if fertilisation and oviposition takes place, but up to 48 or even 72 hours if no males are available.

The eggs are pushed in between the glumes and are deposited on their inner faces. The ovipositor does not pierce any part of the floret. The larvae hatch in about 8 days or less if the weather conditions are favourable. They feed on the sap which is to form the kernel and so (except when only one or two larvae are present) prevent the formation of any corn; this is one of the biological cha-

Table I. *Frequency of* Contarinia tritici *larvae per corn of wheat*, 1927–31.

	In 5560 occurrences				
No. of larvae	Occurrences	No. of larvae	Occurrences	No. of larvae	Occurrences
1	212	24	55	47	7
2	246	25	62	48	5
3	243	26	54	49	2
4	246	27	34	50	2
5	277	28	30	51	1
6	270	29	40	52	4
7	281	30	30	53	1
8	272	31	25	54	1
9	305	32	24	55	1
10	305	33	26	56	2
11	322	34	12	57	3
12	267	35	13	58	2
13	269	36	14	64	1
14	280	37	12	65	1
15	215	38	8	66	1
16	228	39	11	68	1
17	166	40	4	69	1
18	165	41	9	75	1
19	129	42	6	81	1
20	98	43	4	83	1
21	96	44	5	85	2
22	74	45	5	88	1
23	64	46	4	91	1

racters which serve to separate this species from *S. mosellana*. The larvae also are to be found in considerable numbers in each attacked corn. This is the second distinguishing biological character. Table I shows the frequency of number of larvae per kernel. This number depends on the quantity of eggs laid in any one floret, this again being influenced by the amount of wind present at the time of oviposition. It also depends on when the sample is taken, for if the larvae have started leaving the kernels, the numbers will naturally be lowered.

The larvae have attained their maximum size by about 4 weeks after oviposition and then, unless the weather is very dry, they migrate by "jumping" to the soil. Scarcely any larvae remain in the ears, as is shown from the examination of ears plucked at the time of harvest. They remain in the surface

3 in. of soil in a semi-quiescent state until the following spring. Then they become more active and pupate about 8 days to a fortnight previous to the ears of wheat breaking their sheaths. Emergence takes place as previously stated.

This is the normal life cycle. Occasionally, however, a partial emergence takes place in August and September the same year as the eggs are laid. Something under 10 per cent. of the total number of adults emerge in this way. This emergence in September has also been noticed by Kirby (1798). Whether these individuals can exist on wild grasses or not is being investigated. Wagner (1866) states that under such circumstances they have no choice but to oviposit on couch grass (*T. repens*). He also states that midges emerging before the wheat flowers appear oviposit on the more precocious rye. This species is also reputed to attack barley.

While ovipositing the midges are very engrossed in their work and are exceptionally vulnerable. The Empid fly, *Tachydromia pallidiventris* Mg. (kindly identified by Mr J. E. Collin), was caught while eating egg-laying females on Broadbalk, Harpenden, in June and July, 1927. Adult *Trombidium* sp. have also been observed sucking the abdomens of this midge while on the ears of wheat. Curtis (1860) quotes *Empis livida* Linn. as being an enemy of this species.

(*b*) *S. mosellana.*

The life cycle of this species is almost identical with that of *C. tritici*. The exact method by which the larvae leave the ears is not yet known. There are, however, three points of difference which may be mentioned. Firstly, the larvae feed on the surface of the kernel as it is being formed, but do not enter it, and so cause shrunken corn. Secondly, it is usual to find only one or two larvae present on one kernel. This is clearly shown in Table II.

Table II. *Frequency of* Sitodiplosis mosellana *larvae per corn of wheat*, 1927–31.

In 10,605 occurrences					
1 larva	was	found	on a single corn	7655	times
2 larvae	were	,,	,,	2011	,,
3	,,	,,	,,	634	,,
4	,,	,,	,,	199	,,
5	,,	,,	,,	59	,,
6	,,	,,	,,	29	,,
7	,,	,,	,,	13	,,
8	,,	,,	,,	3	,,
9	,,	,,	,,	1	,,
10	,,	,,	,,	1	,,

The third difference in life history is that no secondary partial emergence has yet been observed. This species has been observed to oviposit on slender foxtail grass (*Alopecurus myosuroides*). Other workers have stated that this species also attacks rye, barley and oats. Experiments are being undertaken

to determine the range in host plants of both *C. tritici* and *S. mosellana*. Adult *Trombidium* sp. have been observed eating ovipositing females at Harpenden.

Occasionally both species of larvae are found in a floret. The frequency of this occurrence seems to depend on the intensity of the population as is shown in Table III.

Table III. *Frequency of larvae of* Contarinia tritici *and* Sitodiplosis mosellana *occurring in the same floret of wheat.*

Year	Total occurrences of *C. tritici* and *S. mosellana*	No. of times when both were found in the same floret	Percentage corn attack by both species
1927	811	3	3·2
1928	1689	6	6·5
1929	1868	10	7·7
1930 F*	2243	26	17·1
1930	3821	38	18·0
1931	5733	37	21·4

* 1930 F = sample taken from the first crop after fallow for 2 years. 1930 = sample taken from third successive crop after fallow for 2 years. See section VI (iii).

(*c*) *Distribution.*

Until very recently writers on wheat midges did not differentiate between the two species although Wagner (1866) made the differences quite clear. It was advisable to attempt to find out the distribution of the two species in the British Isles. Previously confirmed records are as follows: both species in Cambridge (1927); Kent (1926); *S. mosellana* only in Pembrokeshire (Anon. 1908), Norfolk (1927), Suffolk (1927), Rutland (A.R., 1927), Sussex (Brit. Mus. Nat. Hist. specimens), Leicester (A.R., 1927), Lincoln (A.R., 1927), Nottingham (A.R., 1927) and Derby (A.R., 1927). Accordingly a systematic survey has been started. Samples from the following counties in England have revealed larvae of both species in 1930: Bedford (H.C.F.N.), Devonshire (W.E.H.), Durham (R.A.H.G.), Gloucester and Hereford (C.L.W.), Monmouth (H.W.T.), Northamptonshire (N.C.), Somerset (C.L.W.) and Yorkshire (T.H.T.). But one sample from Northumberland (R.A.H.G.) gave only a 2 per cent. ear attack by *S. mosellana*, while another gave completely negative results for both species. Likewise both species were absent from a sample from Cumberland (R.A.H.G.). Three samples from Glamorgan (H.W.T.) showed both species present in each, but one sample from Cardigan (J.R.W.J.) and another from Denbigh (W.M.D.) only revealed *S. mosellana*. From Scotland one sample has been received, from Kincardine (G.M.), and *S. mosellana* only was present. In eight samples from Co. Armagh, Co. Derry, Co. Down, Co. Fermagh and Co. Tyrone (per S.P.M.), *S. mosellana* was found in one sample from each of the following three counties, Armagh, Derry, and Fermagh. *C. tritici* was found in none of the Irish samples. It will be of some importance to continue

the matter in order that one can find out definitely if *C. impunctatus* is really absent from Ireland, Scotland, and parts of Wales and the north of England and if *S. moselleana* is truly absent or scarcer in Ireland.

V. Emergence.

At Wye Kerr observations were made in 1934 to determine at what time in the day emergence takes place. Midges of both species were found to be most numerous on the wheat ears about 7.30 p.m. (summer time). All times are given in summer time. Emergence, however, started late in the afternoon and continued until about 2 a.m., at which time the day ends. After this and during the day midges were to be found on the walls and leaves of the wheat. It was noticed that there is a definite sleeping period.

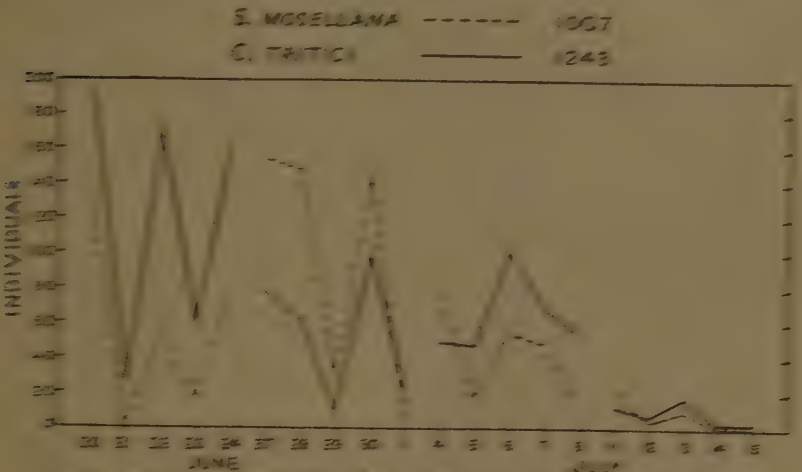

Fig. 2. The numbers of *C. tritici* and *S. moselleana* emerging at Swanwick, Hants.

Observations were made at Rothamsted in 1937 to determine the duration of the emergence period. The method adopted was to walk round the different parts of wheat on Broadbalk continuously from 6 to 9 p.m. and to collect with a net pairs which had been commencing mating. All the females observed emerging. These were afterwards counted. It is to be understood that the numbers so obtained are only relative. This procedure was carried out 5 days a week for 4 weeks. In this way it was possible to estimate the duration of the emerging period. The time chosen was that when the greatest number of midges would be emerging. This experiment was started the day after numbers were low and ended when the end of emergence was approaching.

Fig. 3 shows the results of these observations. It will be seen that the emergence of *S. moselleana* is a week later than that of *C. tritici*. This is

corroborative of the fact that the larvae of *C. tritici* prevent corn formation, while those of *S. mosellana* feed on the developing corn.

The fluctuations in numbers from day to day are very marked. Table IV shows the effect of weather on the numbers ovipositing. It can also be shown that there is a partial correlation with the direction and strength of the wind and the temperature of the soil and air. Humidity and barometric pressure should also be taken into account, but, from the present observations, do not

Table IV. *Effects of weather on numbers of females ovipositing.*

Date	Weather, 6.45 p.m. to 8.15 p.m. (standard time)	Nos. of ovipositing females of	
		Contarinia tritici	*Sitodiplosis mosellana*
June 20	Cloudy, sultry, scarcely any breeze	196	132
,, 21	Cloudy, cold, south-west gusty wind	26	1
,, 22	Sunny, not so cold as last night, slight breeze	170	51
,, 23	Bright sunny intervals, heavy clouds, cool, strong to light south-west wind	59	17
,, 24	Dull, sultry, followed by heavy thunder shower	162	75
,, 27	Dull, sultry, rain threatening, very heavy shower 5.45–6.10 p.m.	78	154
,, 28	Sunny and cloudy, no breeze, thundery but no rain	62	148
,, 29	Heavy rain, very wet, cool breeze	9	32
,, 30	Bright sun, no breeze, heavy rain till 1 p.m., none after	100	143
July 1	Sun at intervals, cool, strong breeze	22	5
,, 4	Dull, sultry, hot	49	77
,, 5	Sunny, sultry, slight breeze	47	18
,, 6	Dull, sultry, hot, with slight drizzle at intervals	101	54
,, 7	Bright sun, cool, no breeze, heavy thunder showers in afternoon	69	48
,, 8	Dull, sultry, thunder shower 5.30 p.m., ears still wet, slight breeze at 7.45 p.m.	54	13
,, 11	Dull, sultry, hot, heavy thunder shower 4–6 p.m.	12	24
,, 12	Scotch mist, slight drizzle, hot, heavy clouds, rain late afternoon	6	3
,, 13	Dull, heavily overcast, fine, rather cooler	17	9
,, 14	Dull, overcast, wet, stopped raining about 7.30 p.m.	2	1
,, 15	Dull, slight breeze, cool	2	0

seem to be of major importance. Sultry nights seem to be the most favourable to the ovipositing midges.

At the height of oviposition literally swarms of the yellow (*C. tritici*) and orange (*S. mosellana*) midges can be seen hovering in clouds over wheat fields. The actual date sometimes varies from one year to another: for instance Shirreff (1873) noticed midges on the wing on June 21st in 1829 (*sic*), from June 10th ("wheat flies first seen tonight") to June 17th ("flies innumerable") in 1871, and from June 29th (first seen), July 4th ("great numbers") to July 23rd

(last seen) in 1872. The observations of the writer tend to show that the actual date does not vary very much as a rule. Thus in 1926 the crest of oviposition was about June 30th to July 1st at Wye, Kent; in 1927 it was on June 20th on Broadbalk, Hertfordshire. The crest of emergence in 1929 in this latter locality was on June 20th, in 1930 June 15th and in 1931 June 16th.

VI. Sampling on Broadbalk.

(i) *Methods.*

Since oviposition continues for something over 5 weeks and the larvae remain in the ears only about 4 weeks, it is obvious that samples taken on any one day cannot give the total infestation of the crop. It was decided, owing to the vast labour of examining the wheat ears, that sampling could only be done once a season and to take the sample when the maximum number of larvae would be present at any one time. This was determined as about 3 weeks after the crest of oviposition. Thus in 1927 the sample of wheat ears was taken on July 13th, 23 days after the crest of oviposition on June 20th. The crest of *C. tritici* was chosen rather than that of *S. mosellana* as the larvae of the former spend a slightly shorter time in the ears.

The plan of gauging the correct day for sampling by the method of finding the crest of oviposition proved to be too exacting and so another method was evolved. From 1928 onwards the larvae obtained in the sampling were reared in the insectary. The daily emergences observed were checked with field observations and so the crest of emergence was found. As the midges oviposit almost immediately after emerging, it was decided to consider the date of the crest of emergence as coinciding with that of the crest of oviposition. In this way the correct date for sampling was determined. Table V shows the method of obtaining the correct date for sampling.

Table V. *Method of obtaining the correct date for sampling.*

Year	Crest of oviposition or emergence	Allow about 3 weeks interval	Date for sampling
1927	June 20	23 days	July 13
1928	—	—	,, 16
1929	,, 20	25 ,,	,, 15
1930	,, 15	23 ,,	,, 8
1931	,, 16	23 ,,	,, 9

The annual sample was taken on Broadbalk and consisted of 500 ears of wheat. This field has been a classical experiment on differential manuring for many years, and advantage was taken of this fact. The whole sample was divided into ten smaller samples of fifty ears each, and it was decided to choose ten of the wheat plots with a view to investigating whether differential manuring of the plant affected the incidence of attack. The following plots were selected.

Plot	Treatment
2	Dung
3	Unmanured (since 1839)
5	Complete minerals
8	Complete minerals + 618 lb. sulphate of ammonia (S./A.)
10	412 lb. S./A. only
11	412 lb. S./A. + 3½ cwt. super
12	,, ,, + 366 lb. S./Soda
13	,, ,, + 200 lb. S./Potash
14	,, ,, + 280 lb. S./Magnesia
16	Complete minerals + 550 lb. nitrate soda

These plots have been manured each year in the same way since 1847, excepting plot 16 which has only received this dressing since 1906.

The actual process of sampling was to walk up one side of each plot, across the top, and down the other side, picking one ear of wheat at given intervals. The frequency of picking the ears was calculated roughly to enable fifty ears to be plucked by the time each plot had been walked round once. It is admitted that the sample was only representative of the outside arm's length of each plot. The ears from each plot were put into separate paper bags and examined in detail as soon as possible. This examination has taken on an average 4 hours a day for a fortnight of 6 working days or about 50 hours to complete. The procedure has been for the writer to examine ear by ear and floret by floret dictating to an assistant who writes down the numbers. It is impossible to work continuously for more than about 2 hours, as the eye strain of the examiner and the monotony for the assistant is too great. It takes just over 5 min. to examine one ear.

(ii) *Effect of differential manuring on incidence of attack.*

Fig. 4 shows the percentage kernel infestation by the two species of midges on ten differently manured plots over a period of 5 years. This damage is that suffered by the crop at the time of sampling. Acting on Dr R. A. Fisher's advice it is proposed at some future date to try to obtain data as to the weight of corn from wheat ears that have been attacked compared with that from unattacked ears. With such data and by the use of regression curves it should be possible to find out whether there is any compensating effect or not by the time of harvest. There are two possibilities: the presence of midge larvae on certain kernels in an ear may result in a temporary draining of the sap going to form the other kernels and so a general decrease in weight of corn; on the other hand, their presence and loss in weight of attacked kernels might be compensated for by an increase in the weight of the unattacked ones.

The actual figures of percentage ear and kernel attack, number of larvae present, number of kernels attacked, as well as the total number of kernels, spikelets and blind spikelets at the two extremities of the ear can be found in Tables VIII–XIII.

No constant significant difference in attack due to manuring has been found, either in the amount of nitrogen given to the plant or the amount of

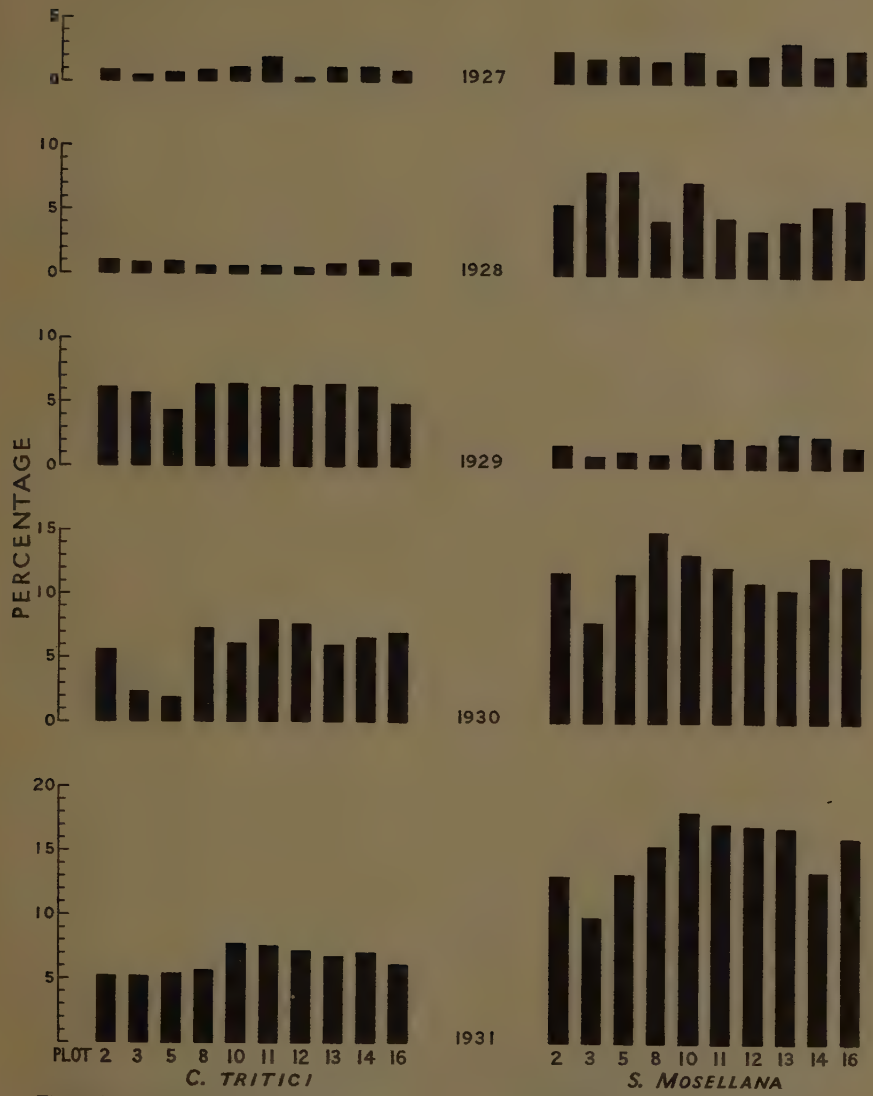

Fig. 4. Percentage kernel infestation by *C. tritici* and *S. mosellana* on ten plots of Broadbalk, 1927–31. The histograms for 1930 represent the average of the two samples taken in that year.

the mineral constituents of the treatment. Although the manurial treatments do affect the time of flowering to some extent there is no corresponding difference in attack by either of the midges. This is to be expected, as the time of flowering is not appreciably altered in relation to the duration of the time of oviposition.

(iii) *General inferences.*

Since the manurial treatment does not appreciably affect the intensity of attack, one can consider the ten samples from the different plots as composing one replicated sample for the whole field. Table VI gives the degree of infestation for the whole of Broadbalk. It can be seen that in the case of *C. tritici*

Table VI. *Degree of infestation or percentage kernel attack by* Contarinia tritici, *and* Sitodiplosis mosellana *on Broadbalk*, 1927–31.

	1927	1928	1929	1930	1931
		C. tritici			
No. of larvae	1,780	2,195	19,265	15,255 21,934 F	19,273
No. of attacked kernels	239	203	1,434	1,157 1,630 F	1,701
Percentage attacked	0·95	0·79	5·9	5·4 6·3 F	6·4
		S. mosellana			
No. of larvae	715	2,043	587	3,659 3,832 F	6,027
No. of attacked kernels	541	1,486	434	2,664 2,856 F	4,032
Percentage attack	2·2	5·7	1·8	12·6 10·8 F	15·0
No. of kernels in sample (500 ears)	24,555	25,735	24,342	21,115 25,940 F	26,857

after 2 years, when the attack was low (about 1 per cent.), there was a decided increase in intensity which remained nearly constant (about 6 per cent.). The fluctuations of *S. mosellana* were of a different nature. In the 5 years under consideration the attack varied from about 2 per cent. in 1927 to about 5½ per cent. in 1928, then decreased to about 2 per cent. in 1929, and rose to about 11½ per cent. in 1930 to 15 per cent. in 1931. It is evident that each of these species responds in a different manner to the factors at work.

It may be pointed out that in 1926 and 1927 one-half of Broadbalk was left fallow and in 1928 and 1929 the other half was left fallow. Consequently the sample of 1928 was of the first crop of wheat after 2 years fallow, that of 1929 of the second crop after 2 years fallow. Two samples were taken in 1930: one from the top half of the field, being of the third crop after 2 years fallow, and the other (F) from the bottom half of the field[1], being of the first crop after

[1] In this case twenty-five ears constituted a sample from a plot instead of fifty as in each of the other samples. In Table XII, the actual figures are used, but in Table VI they are doubled for sake of uniformity.

2 years fallow. In 1931 the sample was taken from the whole field irrespective of the fallowing operations. It will be seen that the numbers of kernels in the two samples taken of the first crop after 2 years fallow were 25,735 and 25,940, the number in that of the second crop 24,342, and in that of the third crop 21,115. This indicates a steady decrease in the yield following successive cropping.

Another inference which may be drawn is that such a study as this only begins to show interesting results after a period of 5 years, and that it is highly desirable that it should be continued for a much longer period.

It would also be of great practical importance if this study, instead of being confined to one variety of wheat (Standard Red) in one locality, could be made to include several varieties from various parts of the British Isles. The sampling method now adopted is one that could be put on a routine basis and not suffer very much. But few individuals would have time enough to carry out this method. Bearing this in mind the data obtained was examined in order to see whether by taking the percentage ear attack one could estimate the percentage kernel attack. It was found that in the case of *C. tritici* up to about 65 per cent. of ear attack represented up to 3 per cent. kernel attack, and from about 70 to 92 per cent. ear attack represented 4–9 per cent. kernel attack. In the case of *S. mosellana* up to 65 per cent. ear attack represented up to about 3 per cent. kernel attack, about 70–90 per cent. ear attack represented 4–7 per cent. kernel attack, and from 90–100 per cent. ear attack represented 8 per cent. kernel attack upwards. It will be seen that by finding percentage attack of wheat ears one could only estimate percentage kernel attacks very roughly, perhaps three divisions, viz. below 3 per cent., between 4 and 7 per cent. and above 8 per cent.

VII. Parasites.

(i) *Identification.*

Various Hymenopterous parasites are known to attack *C. tritici* and *S. mosellana* (for previous records see Barnes (1927)). Those reared in 1929 from the larvae collected in the samples in 1928 were submitted to the late Dr J. Waterston with the following results. Quoting from a letter, dated November 9th, 1929: "From *C. tritici* you have reared *Isostasius punctiger* Nees, and a species of *Synopeas* which may be *sosis* of Walker. From *S. mosellana* you have bred *Macroglenes penetrans* Kirby...and a very remarkable inostemmine species, which is probably referable to the genus *Brachinostemma* but if so it does not appear to correspond with any of the species at present described in that genus. With this peculiar parasite you have also two apparently distinct species of *Platygaster*, which at present I cannot determine." By the untimely death of Dr Waterston this side of the study was put in abeyance for the time being.

The biology of these parasites remains to be investigated and the exact rôle they play to be determined.

(ii) *Methods and results.*

The midge larvae taken from the samples from Broadbalk have been reared in an outdoor insectary in lamp glasses over pots containing fibre and soil. Besides obtaining the correct date for sampling, this breeding has given figures for the emergence of the parasites. Up to the present all the parasites emerging from each midge species have simply been noted as parasites, no attempt being made to separate the different species. All the material has been kept, however, with a view to obtaining the total number in any one year of each species of parasite. The accompanying graph (Fig. 5) shows the daily emergence in 1930 of the parasites compared with that of the host midge, in this case *C. tritici*. It will be seen that the emergence of the parasites is slightly after that of the host. This appears to be the normal occurrence.

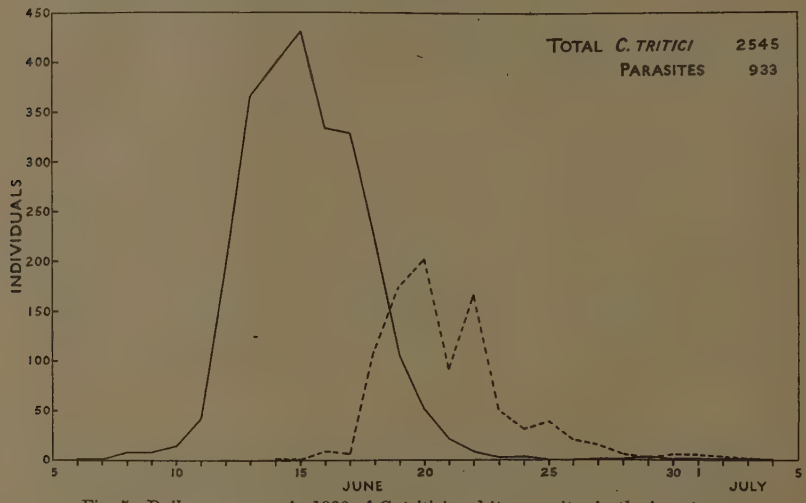

Fig. 5. Daily emergence in 1930 of *C. tritici* and its parasites in the insectary.

The advantage gained by this rearing method is that a figure for the *relative or effective parasitism* is obtained. That is to say the number of parasites which have survived to the imaginal state compared with the number of midges which will be causing the season's attack. It does not give any idea of the number of larvae killed by the parasites.

Acting on the advice of Mr J. C. F. Fryer, it is proposed to examine the relative numbers of midges and parasites emerging from the soil actually on Broadbalk to see whether the figures obtained in the insectary bear any relation to those obtaining in the field.

Table VII shows the relative parasitism figures in the insectary for the years 1929–31, obtained from the previous years samples. It should be explained that all the material of *S. mosellana* collected in 1928 from the ten

plots on Broadbalk was treated as one sample and this resulted in there being one figure for parasitism in 1929. Likewise all the material collected in 1929 was divided into two samples giving two parasitism figures in 1930. In 1930 the material was divided into four samples.

The same applies in the case of *C. tritici* except that in 1929 the material was divided into five samples giving five figures of parasitism in 1930.

Table VII. *Relative parasitism figures, obtained by breeding in the insectary, of* Contarinia tritici *and* Sitodiplosis mosellana *in* 1929–31.

	Samples of relative or effective % parasitism					
Year	1	2	3	4	5	Average
			C. tritici			
1929	10	—	—	—	—	10
1930	5	27	28	39	31	27
1931	38	69	57	54	—	53
			S. mosellana			
1929	73	—	—	—	—	73
1930	40	45	—	—	—	43
1931	69	78	98	92	—	85

It will be seen that there is a significant difference in degree of relative parasitism from year to year.

The histograms (Fig. 6) show the percentage kernel attack on Broadbalk

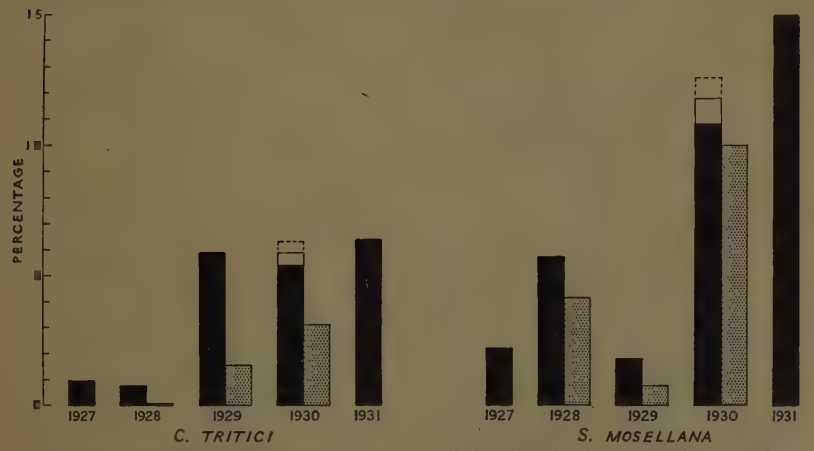

Fig. 6. The percentage kernel attack (solid) on Broadbalk wheat by *C. tritici* and *S. mosellana*, 1927–31 and the relative parasitism percentage for 1928–30 (mechanically stippled).

wheat by the two midges for the 5 years 1927–31 and the relative parasitism percentage for 3 years.

It is proposed to leave the discussion of the parasitism of these two midges until further data has been acquired.

VIII. Summary.

1. A project is explained in which the fluctuations of insect populations in the field are to be studied on a quantitative basis. Three avenues of approach are to be used; the degree of infestation or intensity of attack by the larvae, the degree of parasitism and the dates of emergence (and number of broods). The gall midges are to be used for this study.

2. In this first contribution the wheat blossom midges, *C. tritici* and *S. mosellana*, on Broadbalk have received attention. The fluctuations in intensity of attack over a period of 5 years have been recorded. In the same way the degrees of parasitism for 3 years are noted. The bionomics have been studied over a period of 6 years.

3. The methods employed in sampling and breeding have been explained in detail.

4. A full discussion of the results obtained is being held over until the whole project, entailing similar studies on four additional species of gall midges, has been completed. This should be in 2 years time.

IX. Acknowledgments.

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Table VIII. *Broadbalk wheat*, 1927. *Midge infestation in ears on July 13th.*

Plot	% ear attack		% ear attack by both midges	Total spikelets in 50 ears	No. of kernels in 50 ears	No. of kernels infested		% kernel attack		Total larvae in 50 ears		Av. no. larvae per kernel		Total blind spikelets in 50 ears
	T.	*M.*				*T.*	*M.*	*T.*	*M.*	*T.*	*M.*	*T.*	*M.*	
2	36	54	74	1077	2662	23	63	0·9	2·4	158	74	6·9	1·2	107
3	16	32	46	910	1722	9	32	0·5	1·9	107	33	11·9	1·0	155
5	20	38	52	963	1869	13	38	0·7	2·1	115	53	8·7	1·4	151
8	40	50	66	1017	2533	23	42	0·9	1·7	106	51	4·3	1·2	113
10	52	64	86	1032	2699	33	65	1·2	2·5	193	86	5·8	1·3	84
11	60	40	72	1029	2582	48	30	1·9	1·2	276	43	6·0	1·0	97
12	12	54	58	1028	2459	8	55	0·3	2·2	54	65	6·9	1·2	109
13	38	56	85	1077	2574	28	82	1·1	3·2	226	110	8·0	1·3	131
14	44	52	87	1035	2752	32	61	1·2	2·1	335	93	10·5	1·5	100
16	30	60	81	1081	2703	22	73	0·8	2·7	210	107	9·5	1·5	127

Table IX. *Broadbalk wheat*, 1928. *Midge infestation in ears on July 16th.* (*First wheat crop after 2 years fallow.*)

Plot	% ear attack		% ear attack by both midges	Total spikelets in 50 ears	No. of kernels in 50 ears	No. of kernels infested		% kernel attack		Total larvae in 50 ears		Av. no. larvae per kernel		Total blind spikelets in 50 ears
	T.	*M.*				*T.*	*M.*	*T.*	*M.*	*T.*	*M.*	*T.*	*M.*	
2	26	74	76	1136	2478	25	136	1·0	5·5	224	198	8·9	1·5	119
3	30	96	96	1092	2612	21	211	0·8	8·1	248	288	11·8	1·3	107
5	28	90	92	1123	2669	27	219	1·0	8·2	367	317	13·6	1·5	116
8	20	80	80	1146	2557	15	115	0·6	4·3	130	156	8·7	1·4	112
10	22	90	92	1108	2716	15	198	0·6	7·3	131	274	8·7	1·4	95
11	22	66	68	1121	2573	15	116	0·6	4·6	150	150	10·0	1·3	111
12	18	74	78	1140	2565	14	92	0·5	3·6	133	107	9·5	1·2	109
13	28	72	76	1136	2548	20	110	0·8	4·3	249	155	12·1	1·4	126
14	32	78	82	1108	2441	28	135	1·1	5·5	289	185	10·0	1·4	119
16	28	84	88	1128	2576	23	154	0·9	6·0	274	213	11·9	1·4	117

Table X. *Broadbalk wheat*, 1929. *Midge infestation in ears on July 15th.* (*Second successive wheat crop after 2 years fallow.*)

Plot	% ear attack		% ear attack by both midges	Total spikelets in 50 ears	No. of kernels in 50 ears	No. of kernels infested		% kernel attack		Total larvae in 50 ears		Av. no. larvae per kernel		Total blind spikelets in 50 ears
	T.	*M.*				*T.*	*M.*	*T.*	*M.*	*T.*	*M.*	*T.*	*M.*	
2	88	48	88	1056	2617	161	44	6·2	1·7	2379	69	14·1	1·6	92
3	78	28	84	1042	2611	149	22	5·7	0·8	2675	31	17·8	1·4	100
5	70	40	78	1031	2190	96	29	4·4	1·2	1338	36	13·9	1·2	135
8	78	18	78	1068	2142	137	22	6·4	1·0	1633	30	11·9	1·4	143
10	90	54	96	1053	2460	158	47	6·4	1·9	2175	69	13·8	1·5	111
11	90	56	94	1036	2385	145	55	6·1	2·3	1987	72	13·7	1·3	113
12	86	50	94	1065	2387	151	45	6·3	1·9	1937	56	12·9	1·2	119
13	88	70	96	1103	2611	166	70	6·4	2·7	1918	88	11·6	1·3	109
14	82	48	92	1074	2259	141	56	6·2	2·5	1683	77	11·9	1·4	141
16	74	44	84	1100	2680	130	44	4·9	1·6	1540	59	11·8	1·3	102

Table XI. *Broadbalk wheat*, 1930. *Midge infestation in ears on July 8th.*
(*Third successive wheat crop after 2 years fallow: top half.*)

Plot	% ear attack		% ear attack by both midges	Total spikelets in 50 ears	No. of kernels in 50 ears	No. of kernels infested		% kernel attack		Total larvae in 50 ears		Av. no. larvae per kernel		Total blind spikelets in 50 ears
	T.	*M.*				*T.*	*M.*	*T.*	*M.*	*T.*	*M.*	*T.*	*M.*	
2	78	96	100	1105	2244	120	249	5·3	11·1	1529	354	12·7	1·4	151
3	28	86	86	1022	1928	29	135	1·5	7·0	338	171	11·7	1·3	163
5	22	90	94	1029	1758	20	215	1·1	12·2	260	303	13·0	1·4	179
8	92	98	100	1167	2158	164	369	7·6	17·1	2117	544	13·0	1·5	198
10	86	100	100	1151	2164	131	287	6·1	13·3	1821	382	13·9	1·3	174
11	80	100	100	1106	2130	142	291	6·7	13·7	2027	385	14·3	1·3	171
12	88	98	100	1089	2077	150	255	7·2	12·3	2073	354	13·8	1·4	170
13	80	98	100	1160	2265	138	252	6·1	11·1	1707	355	12·4	1·4	170
14	76	100	100	1127	2149	126	287	5·9	13·4	1738	379	13·8	1·3	179
16	74	100	100	1167	2242	137	324	6·1	14·5	1645	432	12·0	1·3	194

Table XII. *Broadbalk wheat*, 1930. *Midge infestation in ears on July 8th.*
(*First wheat crop after 2 years fallow: bottom half.*)

Plot	% ear attack		% ear attack by both midges	Total spikelets in 25 ears	No. of kernels in 25 ears	No. of kernels infested		% kernel attack		Total larvae in 25 ears		Av no. larvae per kernel		Total blind spikelets in 25 ears
	T.	*M.*				*T.*	*M.*	*T.*	*M.*	*T.*	*M.*	*T.*	*M.*	
2	80	96	100	583	1482	89	181	6·0	12·2	1318	263	14·8	1·5	59
3	76	100	100	564	1322	41	112	3·1	8·5	582	152	14·2	1·4	61
5	64	100	100	575	1233	33	136	2·7	11·0	460	172	13·9	1·3	77
8	88	100	100	604	1302	90	164	6·9	12·6	1290	234	14·3	1·4	78
10	72	96	100	587	1385	83	180	6·0	13·0	1341	239	16·2	1·3	67
11	88	92	100	576	1373	123	145	9·0	10·6	1659	200	13·5	1·4	64
12	88	92	100	575	1201	98	115	8·2	9·6	1040	155	10·6	1·3	87
13	72	92	98	576	1134	66	109	5·8	9·6	668	143	10·1	1·3	103
14	76	100	100	584	1235	89	154	7·2	12·5	1190	187	13·4	1·2	88
16	84	92	96	590	1303	103	132	7·9	10·1	1419	171	13·8	1·3	74

Table XIII. *Broadbalk wheat*, 1931. *Midge infestation in ears on July 9th.*

Plot	% ear attack		% ear attack by both midges	Total spikelets in 50 ears	No. of kernels in 50 ears	No. of kernels infested		% kernel attack		Total larvae in 50 ears		Av. no. larvae per kernel		Total blind spikelets in 50 ears
	T.	*M.*				*T.*	*M.*	*T.*	*M.*	*T.*	*M.*	*T.*	*M.*	
2	84	94	96	1161	3189	166	414	5·2	13·0	2115	625	12·7	1·5	74
3	76	94	96	1079	2305	119	226	5·2	9·8	1441	329	12·1	1·5	140
5	74	100	100	1139	2841	151	376	5·3	13·2	1844	589	12·2	1·6	80
8	90	100	100	1179	2510	140	384	5·6	15·3	1830	596	13·1	1·6	149
10	90	96	100	1147	2566	197	461	7·7	18·0	2336	741	11·9	1·6	135
11	94	98	100	1136	2911	218	497	7·5	17·1	2329	692	10·7	1·4	89
12	90	100	100	1141	2911	210	496	7·2	17·0	2139	760	10·2	1·5	90
13	90	100	100	1162	2465	164	413	6·7	16·8	1788	593	10·9	1·4	149
14	90	98	100	1142	2440	170	326	7·0	13·4	1867	469	11·0	1·4	146
16	86	100	100	1137	2719	166	439	6·1	16·1	1584	633	9·5	1·4	125

NOTES ON THE FRUIT BATS (*PTEROPUS* SPP.) OF AUSTRALIA

By FRANCIS RATCLIFFE, B.A.

(*With Plates I–IV.*)

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I. Introduction.

The information contained in these notes was collected during an investigation carried out for the Commonwealth Council for Scientific and Industrial Research during the years 1929–31. The full report of the work has been published by the Council as *Bulletin* No. 53. The main area covered in this investigation lay between Port Douglas in north Queensland and Bulli, some 60 miles south of Sydney, New South Wales, and usually not more than 50 miles inland, except near the Queensland-New South Wales border and in central Queensland. The western limits of operations were Longreach, Eidsvold, and Stanthorpe in Queensland, and the northern tableland (Tenterfield, Glen Innes) in New South Wales.

II. The Australian species of *Pteropus*.

There are four species of *Pteropus* found on the Australian mainland, while a fifth has been described from a group of islands off the coast of Queensland. They are described in detail by Knud Anderson (1912).

(1) Pteropus poliocephalus *Temminck*.

Range. Along the coastal belt from central Queensland to the Victorian border.

Phot. 2. *Pteropus goudii* (male).

Phot. 1. *Pteropus goudii* in characteristic resting position.

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Face p. 33

Colour. Body dark grey, usually with rather a grizzled appearance, due to an admixture of light-tipped hairs. Head also grey, usually distinctly lighter than the body. "Mantle" and forepart of the breast reddish yellow. (The mantle is the patch of fur extending from about the base of the ears to the shoulder blades, which, in a large majority of the species of this genus, is brightly coloured in marked contrast to the fur of the body.) A few young individuals were collected in which the body colour was a light silver-grey, and the mantle and collar almost lemon-yellow. *Fur.* Long and soft in comparison with the other Australian species, and extending on to the legs as far as the ankles. *Size.* Forearm (which in fruit bats is usually slightly under one-sixth of the wing spread) up to 165 mm. One of the largest individuals shot, a male, measured just under 4 ft. from wing-tip to wing-tip, and weighed 2 lb. Unfortunately the forearm of this specimen was not measured. *Young.* Born with distinct mantle and collar, though of duller colour than in the adult.

Identification in the field. This is the only Australian species in which the light-coloured fur completely encircles the neck. It is readily distinguished by its "furry" appearance and this "ginger" collar, which is prominently displayed when the animals hang head downwards in the daytime.

(2) Pteropus gouldi *Peters* (*Pl. I, photos.* 1 *and* 2).

Range. Along the coastal belt of Queensland, north of the Mary River, of the Northern Territory, and northern West Australia.

Colour. Uniformly black, sometimes showing a grizzling of lighter hairs. Mantle dark rusty red or chocolate to yellowish (the latter in old individuals). Occasionally there are brown markings on the face, particularly round the eyes. *Fur.* Short and rather hairy, extending on the leg only to the knee. *Size.* Slightly larger than *Pt. poliocephalus*, forearm up to 180 mm. *Young.* Born completely black, with no sign of light mantle. Even in almost fully grown specimens the fur may have to be ruffled to discover a reddish tinge.

Identification in the field. Although there is more variation in this than in any other of the Australian species, due chiefly to the alteration of the mantle colour with age, it is usually distinguishable because it really looks black. Certain individuals, however, approach *Pt. conspicillatus* (below) rather closely, having an extensive light mantle, and quite well-defined "spectacles."

(3) Pteropus conspicillatus *Gould.*

Range. Cape York Peninsula, south to Cardwell, also New Guinea. *Colour.* Body black, similar to *Pt. gouldi*, but with the grizzling perhaps more frequent and pronounced. The mantle, which extends to slightly in front of the ears, pale yellowish or straw-coloured. Rings of pale yellowish fur round the eyes (from which this species derives its common name: the Spectacled Fruit Bat). In many individuals this pale colour extends over the cheeks and on the top of the nose, and as the dark fur of the face is generously shot with

light shining hairs, the head appears to be very much lighter than the body. *Fur.* As in *Pt. gouldi*. *Size.* Perhaps slightly larger than *Pt. gouldi*; forearm up to 181 mm. *Young.* Born with distinct mantle, the fur of which is very light, and has a pretty sheen. (Thus in the young stages there can be no danger of confusion between this and the preceding species.)

Identification in the field. The well-defined "spectacles" and the pale mantles, more extensive than in *Pt. gouldi*, and very uniform throughout the species, usually make its identification easy.

(4) Pteropus scapulatus *Peters.*

Range. Similar to *Pt. gouldi*, but extending further inland, and south to the Victorian border.

Colour. Uniform reddish brown or light chocolate. No distinctly coloured mantle. The slight differences of colour, i.e. on the crown of the head and round the neck, shade gradually into the general body colour. Crown of head tends to be mousey grey. The fur round the neck is longer than on the body, and looks rather lighter. Long soft hairs on the underside of the wing membranes near the body are pale straw-coloured or lemon-yellow. *Fur.* Short, soft, and close, with almost a mole-like texture. *Young.* On no occasion were newly born young observed. *Size.* Markedly smaller than the three species described above. Forearm from 120 to 143 mm.

Identification in the field. The small size and uniform reddish colour make this species unmistakable. In flight they are easily distinguished from the three larger species by the greater transparency of their wing membranes.

(5) Pteropus brunneus *Dobson.*

There have been no reliable records of this species since the type specimen (from the Percy Islands) was described in 1878. Its only claim to be considered a member of the Australian mainland fauna is the statement by Broadbent (Anderson, 1912, p. 150) that he observed "a camp of *Pteropus brunneus*" flying over the coast opposite the Percy Islands—which are nearly 100 miles to the east! This record is open to the very gravest doubt.

The genus *Pteropus* covers a very wide range geographically, being found in most of the islands in the tropical belt between Madagascar in the west, Formosa in the north-east, and Samoa in the south-east, and also in India, the Malay Peninsula, and Australia. The centre of dispersal of the genus, judging by the distribution of the various species among the geographical regions and sub-regions (as defined by Wallace), was Austro-Malaya, "or rather an area much larger than, but including Austro-Malaya, and probably excluding Australia" (Anderson, 1912, p. 83).

The eighty-two species of the genus *Pteropus* are arranged by Knud Anderson in seventeen groups, according to their probable natural affinities.

(Since the publication of the British Museum Catalogue in 1912, eleven new species and two new sub-species of the genus *Pteropus* have been described by Sanborn, 1931.) Each of the Australian species is placed in a different group, which means that individually they are more closely related to forms occurring outside the continent than they are to one another. Thus *Pt. poliocephalus* is a peculiar modification of a New Guinea type; *Pt. gouldi* is very closely allied to *Pt. alecto*, of Celebes and Lombok; and *Pt. scapulatus* has its closest relative in the Solomon Islands. *Pt. conspicillatus* actually occurs in south-eastern New Guinea as well as in Australia, and in addition possesses a very close relative in *Pt. chrysauchen*, which replaces it in the northern and western parts of that island.

It must be assumed, therefore, that the ancestors of the Australian species of *Pteropus* colonised the continent from the Austro-Malayan islands, arriving by the New Guinea-Cape York route. (The distribution of *Pt. conspicillatus* at the present day is in itself most suggestive.) They did this at a period sufficiently remote to allow for the modifications which have given rise to the Australian species in their present forms. Of these species *Pt. poliocephalus* and *scapulatus* "are decidedly the most peculiarly modified" (i.e. in relation to their closest relatives), and were therefore probably the earliest immigrants into the continent. In this connection it is interesting to note that these two species alone have succeeded in pushing south of the Queensland-New South Wales border.

III. THE ENVIRONMENT.

Fruit bats are found in eastern Australia from Cape York (lat. 11° S.) to the Victorian border (35° S.). Conditions along the north coast, where *Pt. gouldi* and *scapulatus* occur, were not studied during the investigation. By far the greater part of the population is limited to the coastal belt, i.e. within 100 miles or so of the sea, which is a region of comparatively high rainfall. (The isohyets run roughly north and south, the precipitation decreasing to the west.) Although this range comprises a strip of country some 2000 miles long, extending from the tropics to the temperate zone, the main type of vegetation which occurs in it is remarkably uniform. It is a more or less continuous belt of forest, varying from open parkland to forest proper. The lack of variety is due to the dominance of the genus *Eucalyptus*, different species of which are adapted to the different climatic conditions found throughout the belt.

Rain forest, or jungle (Pl. II, phot. 4) is found in patches of varying size as far south as the Hunter River in New South Wales, about 100 miles north of Sydney. Compared with the "open," or Eucalypt, forest from which it is usually sharply delimited (Pl. II, phot. 3), the total area of rain forest is small; moreover the rain forest has suffered to a relatively greater extent from clearing for cultivation. Considerable tracts are still to be found in the north (e.g. the Atherton Tableland), and in the ranges of the Queensland-New South Wales border. Otherwise it occurs mostly as relict patches of limited area.

Apart from the different forms of rain forest (which is a community subject to great local variation), the *Eucalyptus* forest of the coastal belt is interrupted locally by patches of other vegetation types. Of importance to the fruit bat population are the Tea-tree and mangrove swamps. Tea-trees (*Melaleuca* and *Leptospermum* spp.) provide the bats with both shelter and food, the latter in their heavy crops of blossom. They are found along all the numberless watercourses, besides growing densely in swampy areas (Pl. IV, phots. 7 and 8).

It is safe to say that every creek and river on the Queensland coast (and most of those in New South Wales, north of Sydney) has, to a greater or lesser extent, a growth of mangroves at or near its mouth (Pl. III, phot. 5). Southward from the Mary River, in Queensland, the mangroves form only fringing growths of limited depth; though in the shelter of islands the growth may be fairly extensive. North of the Mary River the mangroves occur to an increasing extent, often forming tracts of great area. This is probably due to the shelter provided by the Barrier Reef, and also to the predominance of *Rhizophora mucronata*, a species which can flourish in the breaking waves of the open sea, and by the gradual accumulation of silt and mud round its roots, helps to form "swamps," often many hundreds of yards deep, in suitable localities.

In Queensland, along the western edge of the coastal belt, the forest formation is often very open, approximating to the savannahs found farther inland. Scattered through this parkland are patches of dense vegetation—"scrubs"—which are comparable to the rain forest of the wetter districts. These scrubs, though usually of small size, harbour certain animals which are quite alien to the surrounding forest, e.g. the scrub turkey (*Alectura lathami*), and others which, though they feed in the open forest, depend on them almost exclusively for shelter, e.g. certain wallabies (*Macropus* spp.). Fruit bats, in their relation to the vegetation types found along the coastal belt, are comparable to these wallabies. For food they depend primarily on the open (*Eucalyptus*) forest association, while for shelter they turn to the dense vegetation of the rain forest and the swamps, and of the "scrubs" of the savannah country.

IV. Habits.

(*a*) *General.*

Fruit bats are nocturnal and gregarious. In the daytime they hang together in large numbers on the branches of trees. In Australia these congregations are known as "camps." A site once selected is usually occupied regularly, unless the animals are forced to abandon it by external circumstances. Certain camps are known to have existed for upwards of fifty years, in fact as long as the local settlers can remember.

Seclusion and shade seem to be the chief factors influencing the animals in their choice of a camp site. However, when a patch of vegetation has harboured a mob of fruit bats for some time, the upper branches often become quite de-

nuded of leaves, thus providing no real protection from the sun (see Pl. IV, phot. 7). Patches of rain forest (jungle) or mangrove swamp are usually selected. On no occasion was a camp found in the *Eucalyptus* forest. In districts where rain forest or mangrove swamp are not available, camps will be formed in Tea-tree swamps, in scrubs of Brigelow (*Acacia harpophylla*), etc., and in creek-bed vegetation, such as sheoaks (*Casuarina* spp.) or weeping willows.

Being nocturnal, the bats get their necessary sleep in the daytime. Nevertheless the camps are very rarely quiet—in fact they are most easily located by their sound. The animals are very quarrelsome, and much of the day is spent in noisy bickering. In very hot weather they are quieter, most of their energy being used in fanning their wings as they hang in camp.

Fruit bats are very efficient climbers, using their clawed and jointed thumbs as well as their hind limbs. *Pt. scapulatus* especially clambers about the trees with great agility, and when disturbed will usually climb upwards before taking wing. The flight of the bats is easy and gliding, the older individuals being noticeably more efficient.

Fruit bats are undoubtedly intelligent. They are wary in camp, and seem to learn rapidly from experience, e.g. of shot guns (a camp which has been "shot up" once or twice will take flight at the mere approach of an observer). Three times during the investigation the habit of individual bats keeping an intruder to their camp under observation was met with. These "spies" evidently realised the powers of a gun (in fact several were noticed with shot-holes in their wing membranes), and gave very few opportunities of a shot. In one case a single individual (of *Pt. gouldi*) followed me for over an hour, even into that part of the camp (which covered over 10 acres) occupied solely by another species (*Pt. scapulatus*).

The camps "break" soon after dusk. The flight is orderly. One or more streams of bats are formed, which fly away, usually at a considerable height, and in a most purposeful manner. (A large camp may take nearly an hour to empty itself.) In addition to the main column, or columns, a large number of individuals fly away without any semblance of order or definite purpose. These "scouts" fan out in all directions, and at a much lower altitude. Thus in addition to the feeding ground favoured at the moment, the whole of the camp's "territory" will be explored fairly regularly. It is thus easy to understand why no fruit can ripen, or trees come into blossom, within feeding range of a camp without being quickly discovered by the bats. It was not possible to discover how far the bats would fly in search of food. A radius of 25–30 miles at least would seem possible for animals with such a strong and steady flight; but when bats were observed feeding in an apparently isolated spot, it was never possible to assert that there was no camp within that distance. As the average distance between camps (in Queensland) is rather under 25 miles, it would seem that a 10–20 mile radius would include the normal feeding area of a camp.

Whether or not there is conscious communication between individuals, so

that the discoveries of the "scouts" can benefit others, it is difficult to say. Fruit growers, who see increasing numbers of the bats visiting their orchards nightly, as soon as the first individual raider has made its appearance, are convinced that there is. On the other hand, this could be simply explained if the animals had the habit, once their particular source of food began to fail, of following those individuals which flew straight to a previously discovered feeding ground when the camp broke of an evening. The direction of the main flight from the camp will continually alter during the course of the season, the original stream gradually dwindling as a second column, flying in some new direction, increases.

In their search for food the bats are undoubtedly guided principally by their sense of smell. Their attacks on cultivated fruit are most severe on still, damp nights, when conditions for scent would be ideal. Bee-keepers state that after they have been separating honey, and the air is charged with the sweet smell, fruit bats would often screech round the house all night, although there was neither fruit nor blossom to attract them. Moreover, once a fruit has been bitten into it will prove an attraction to bats on subsequent nights, the broken skin presumably liberating the scent. Growers who poison take advantage of this. I have heard of as many as seven bats being poisoned on a single paw-paw in one night.

The three larger species are very similar in their habits, such differences as exist, apart from slight food preferences (see below), can be attributed to their climatic environment. *Pt. conspicillatus*, *gouldi*, and *poliocephalus* seem to fill identical niches in (*a*) the tropical, (*b*) tropical and sub-tropical, and (*c*) sub-tropical and temperate regions of eastern Australia respectively. *Pt. scapulatus* has to be considered separately, for it differs from the other three species in so many ways. It is smaller; its dentition is peculiar, the cheek teeth being very small and narrow (which probably explains its specialisation as a blossom-feeder); its breeding season is "reversed" (see below); its range is much wider, embracing districts with a different type of vegetation from that found in the coastal belt, and its movements are more erratic than those of the other species (see below); it is markedly less intelligent than the larger species. It is much less wary in camp (the aboriginals used to kill it with sticks and spears). Its evening flights are very regular, with hardly any sign of individual "scouting" (records of fruit bats dying in large numbers, apparently from lack of food, seem to be limited to this species). In addition it has several little peculiarities which make it possible to identify this species in reports of observant people who describe their camps, e.g. its habit of clustering in vines and the undergrowth.

(*b*) *Parasites.*

During the investigation specimens were examined for parasites. The only ectoparasites met with were the highly specialised, wingless Nycteribiid flies

Phot. 4. Clearing in typical rain forest in south Queensland.

Phot. 3. "Open" (*Eucalyptus*) forest. Blue gums (*E. tereticornis*) in foreground.

of the genus *Cyclopodia*. The only species hitherto recorded from Australia is *C. similis* Speiser, 1900 (= *pteropus* Rainbow, 1901); but Mr A. Musgrave, of the Australian Museum, who has examined my specimens, states that some of them belong to a second species, with which he proposes to deal at a later date.

Of the four species of fruit bat, *Pt. scapulatus* is by far the most heavily infested, up to two dozen being sometimes found on a single individual. Specimens of *Pt. gouldi* and *conspicillatus* were rarely, if ever, found to be free. *Pt. poliocephalus* were comparatively lightly infested, so that frequently no parasites could be obtained from any of the specimens shot in a camp.

No special search was made for endoparasites, though if present in the gut, at any rate, they would almost certainly have been noticed during stomach examinations. None were found in adult individuals. In the case of suckling young (*Pt. poliocephalus*) one or more Nematode worms (unidentified to date), 3–4 in. long, were found in the small intestines of several specimens.

(*c*) *Reproduction.*

As a rule one young one alone is produced at birth, there being only one breeding season per year. Twins have been reported, but were not once met with during the investigation, although great numbers of breeding animals were observed. I was informed that in one camp, against which a shoot was arranged some years ago, a considerable number of the females shot were carrying twins. The females have a single pair of mammae, which are thoracic, being situated almost in the region of the armpit. As soon as it is born the young one clings to its mother, using the claws of its thumbs as well as its hind-feet, but chiefly depending on its mouth, which retains a most tenacious grip on one or other of the teats. The testes of the male are withdrawn, or partially so, during the greater part of the year. On the approach of the breeding season they are protruded rather obviously in a naked scrotum.

(In *Pteropus* the structure of the pelvic girdle differs in the two sexes. Whereas in the male the normal symphysis is found, in the female the ischio-pubic bones do not even converge ventrally. This is presumably an adaptation to permit the development *in utero* to reach a stage at which the young will have sufficient strength to support itself on the underside of its parent almost indefinitely.)

Once only can it be said with certainty that coition was observed. The male was suspended behind the female, contact taking place between the under parts only.

It is difficult to estimate the period of gestation in the case of the Australian species of *Pteropus*, for the birth of the young was not observed in *Pt. scapulatus*, and this is the only species for which a definite record of copulation was obtained. (In the case of an allied genus, *Rousettus*, studied in captivity, birth took place 15 weeks after the last copulation.) At best the estimate would be very rough, for there is considerable variation between individuals. Thus

embryos from females of *Pt. gouldi* shot in north Queensland on July 30th, 1929, varied from less than 1 in. to over 2 in. in body length, the containing uteri varying from the size of a cherry to that of a large plum. This would probably represent a difference in time of conception of several weeks.

The following facts were, however, established:

(1) Coition in the case of *Pt. scapulatus* occurs in October (observed in the Rockhampton district of Queensland), and probably earlier.

(2) In the case of *Pt. gouldi* and *poliocephalus* the young are born in this (and probably the preceding) month.

(3) Pregnant females of *Pt. scapulatus*, shot in New South Wales on February 1st, contained embryos comparable to the most advanced of those of *Pt. gouldi* collected at the end of July. Therefore it may be inferred that birth in the case of *Pt. scapulatus* takes place in April.

(4) By March and April the testes of *Pt. poliocephalus* are obviously protruded, and mating seems to occur.

Thus the breeding season in the case of *Pt. scapulatus* is completely reversed as compared with that of the three larger species. No explanation of this very interesting fact suggests itself. The season of births in the case of the three other species is not coincident. *Pt. gouldi* appears to be some weeks ahead of *Pt. poliocephalus*; and, judging by the growth of the young observed in a camp near Cairns, north Queensland, in early November, *Pt. conspicillatus* in turn must be nearly a month ahead of *Pt. gouldi*. This might be expected, in view of the geographical distribution of the three species. It is probable that even within a single species the breeding season is earlier in the more northern parts of its range. Thus it is recorded by Anderson (1912, p. 372), that in the case of *Pt. gouldi* the young are born in March and April in North Australia, and in August many females have young of considerable size attached to their breasts.

During the later stages of pregnancy, and the period of suckling, the females tend to segregate together in the camps. They are noticeably quiet, and exhibit a marked reluctance to take wing. The reluctance increases as the young one grows, and becomes a greater burden to its parent. When visiting a camp of *Pt. poliocephalus* on January 21st, 1930, I made a note: "Females carrying young almost the size of adult *scapulatus*; carried on the *back* when climbing vertically; mothers reluctant to fly, and were easily shot." On February 4th, also in a camp of *Pt. poliocephalus*, I noted: "Only two females still carrying young." These and other similar observations indicate that the young become independent of their mothers when about 4 months old. (They will begin to hang on the branch beside their mothers, often wrapped in a maternal wing, before this.) It is almost certain, however, that some sort of maternal care is exercised for quite a long time after the young have ceased to be carried. When but 4 months old the young bats are still very feeble flyers.

In the suckling stage the young are carried nightly to the feeding grounds by their mothers. They can easily be distinguished clinging to the undersurface of the females, and the slower flight of these burdened individuals is quite noticeable. What actually occurs at a later stage is not yet clear. On the one hand it is well established that when fruit bats are raiding an orchard the young ones are sometimes left hanging in trees near by, and are periodically brought fruit. (Whether, in this case, they would fly alone from the camp is not known.) On the other hand there is good evidence that the young are sometimes left in the camp at night. Thus a farmer, near Rockhampton, often heard the young bats squealing in a near-by camp at night, and at first mistook them for sucking pigs. I was also informed that in another camp (of *Pt. poliocephalus*) in March and April the bats would return, presumably to feed their young, at about 8 o'clock.

As the species of *Pteropus* are closely related, there would seem to be some possibility of natural hybridisation, particularly as mixed camps are the rule rather than the exception. *Pt. gouldi* and *poliocephalus* are generally found camped together in the area where their ranges overlap—often with *Pt. scapulatus* as well (though the last, with its "reversed" breeding season, can be ignored in this connection). Two individuals were shot, in camps of *Pt. poliocephalus*, whose coloration was intermediate between this species and *Pt. gouldi*. Their dentition, however, was that of *Pt. poliocephalus*, of which they must probably be considered colour varieties.

Pt. gouldi and *conspicillatus* are very closely related indeed. They are placed in different "groups" (see above), which, however, are closely allied. The two groups are distinguishable only by mantle colour, a slight difference in the shape of the ears, and the fact that the dentition, though of identical type, is rather heavier in the *conspicillatus* group. None of these characters are really satisfactory, for *Pt. conspicillatus* has, for its group, a rather light dentition, and thus approaches *Pt. gouldi* in this respect; and *Pt. gouldi*, though normally possessing the dark mantle typical of its group, shows great variation in this character. Moreover, individuals are frequently found which, in addition to having a light golden mantle, show brown markings on the face, similar to, but usually rather darker than, the "spectacles" of *Pt. conspicillatus*. In fact, though the newly born young of the two species are totally different (see above), they tend to converge rather closely.

There were not many chances of observing *Pt. conspicillatus* during the investigation, but it is significant that not once was it met with in a "mixed" camp, although *Pt. gouldi* occurs throughout its Australian range. In a camp of *Pt. conspicillatus* at Cairns an adult male was shot which, had it occurred elsewhere, I should have had no hesitation in identifying, on superficial examination, as *Pt. gouldi*. Moreover, other individuals were secured in this camp which showed perfect gradation between the typical *conspicillatus* (with a considerable amount of pale straw colour on the face) and this *gouldi*-like indi-

vidual, in which the "spectacles" were brown rather than straw-coloured, though the mantle was typically pale.

(*d*) *Natural enemies and number control.*

The potential increase of a fruit-bat population is about 40 per cent. per annum. This figure is based on the assumptions that (1) the potential "natural" breeding life is 10 years (fruit bats have been recorded (Chalmers Mitchell, 1911) as living in captivity for as long as 17 years); (2) that the numbers of the sexes are approximately equal (observations and the records of specimens taken during the investigation indicate this, though in individual camps the equality may be masked by the segregation of the sexes, which seems to take place to some extent after mating); and (3) that the female has one young one every year (100 per cent. pregnancy in adult females was met with throughout the investigation).

There seems to be no evidence that the fruit-bat population of Australia undergoes noticeable fluctuations in size—local increase in numbers and years of unusual attacks on cultivated fruit can probably be explained by variations in migration (see below) and by climatic factors. Therefore it must be assumed that there is a natural check operating which accounts for about 30 per cent. of the population each year.

At first sight it does not seem likely that natural enemies could play an important part in the control of the population, for such animals as attack fruit bats are general predators and carrion feeders, which evince no preference for them as an item of diet. The animals definitely known to attack fruit bats are the following: crocodiles (*C. johnstoni* and probably *porosus*), which snap them up as they fly down to drink; monitor lizards (*Varanus* spp.); carpet snakes (*Python spilotes*); the wedge-tailed eagle and the white-breasted sea eagle (*Uroaetus audax* and *Haliaetus leucogaster*); and probably the other larger birds of prey, including the owls.

As an adult fruit bat is very wary and far from defenceless, it is probable that the toll of predators falls most heavily on the young. If it is a fact that the young, when they are too heavy to be carried long distances, are habitually left behind in the camps, it is probable that large numbers are accounted for by nocturnal predators, and that animal enemies play a more important part in the control of numbers than first appears to be the case.

Records of specimens shot during the investigation indicate that there is a considerable mortality among the young. In the case of females one can tell by the size of the nipples whether or not an individual has bred. "Immature" females, whose nipples are very small, can with some certainty be classed as under 2 years old. In the case of *Pt. scapulatus* (the only species for which reliable numbers were obtained), 47 females were collected in one camp, of which 6 (13 per cent.) were "immature"; in another camp 16 were shot, of

which 3 (19 per cent.) were "immature." For the combined figures the percentage works out as just over 14.

No reliable evidence of the occurrence of epidemics among the fruit-bat population was discovered. Records of considerable mortality were obtained in one or two localities. They all seemed to be attributable to the extraordinary migration of *Pt. scapulatus* in 1926–7, as a result of which large numbers certainly did die, apparently from weakness and starvation. Records of mortality in established camps, as opposed to temporary ones formed by newly arrived migrants, seem to be limited to one in Queensland (Helidon) in 1905, and one in New South Wales (Malanganee) in 1913 (?). These can both probably be attributed to the abnormally high temperatures which prevailed at the time.

(*e*) *Diet.*

The diet of *Pteropus* includes almost all fruit with a pretence to succulence. At times fruit bats of this genus have been stated to eat insects; but there appears to be no evidence for this assertion in the case of the Australian species. Besides the Australian species several forms are known to feed, at times, on blossom; but there is nothing published which indicates that this is a really important item in the diet of fruit bats in other countries.

Unlike most vegetarian animals, fruit bats have a very short intestine, with a correspondingly small abdomen (in fact, in comparison with the thorax, with its special developments connected with flight, it is almost ridiculously small). This is probably due to the fact that the nutriment actually swallowed by the bats is predominantly of a liquid nature. They seem to triturate their food, pressing out the juices of the fruit and the nectar of the flowers, and spitting out, as far as possible, all hard and fibrous matter. (Thus a fruit bat is reported to have succeeded in feeding on peaches, despite the fact that a mosquito net had been spread over the tree, by sucking the fruit through the mesh.) It is natural, therefore, that the process of digestion should be rapid. It was found that, in order to carry out stomach examinations, specimens had to be obtained while still feeding, or immediately on their arrival in their camp at dawn.

At times, of course, some solid matter will be swallowed, e.g. the seeds of berries. When the animals are feeding on blossom, stamens and pollen grains can be found in great quantities in their stomachs and small intestines. The pollen grains are apparently not digested; but, judging by their collapsed appearance, it is possible that they are sufficiently affected by the digestive juices to permit the transfusion of a part at least of their contents. If this is the case, it is possible that pollen may be of importance in the diet of the animals. Nectar and the juices of fruit alone would not seem to provide the nitrogen requirements of their metabolism.

Fruit bats appear to drink regularly, especially when depending solely on a blossom diet. They usually drink on the wing, lapping up the water as they

glide over the surface. Sometimes, however, they will climb down vines, etc., to reach a pool in a rain-forest area.

Practically all varieties of cultivated fruit are known to be eaten by the bats. Their favourites seem to be soft, sweet fruits such as mangoes, peaches and figs. They readily attack apples and pears, and the two northern species (*Pt. gouldi* and *conspicillatus*) will eat citrus, especially mandarins. The part played by cultivated fruit in the diet of the animals was studied in detail, and is discussed at length in the official report of the investigation (Ratcliffe, 1931). After taking into consideration the size of the fruit-bat population, the area under cultivated fruit, the nature of the losses sustained by growers, and the fact that certain varieties (e.g. bananas) were largely immune on account of early gathering, it was concluded that cultivated fruit did not represent an important item in the diet of the fruit-bat population of Australia. On rare occasions in a few districts it might provide a stand-by; but normally "heavy" attacks on orchards and plantations may be considered more as an indication of a temporary shortage of "natural" food.

The fondness of the animals for nectar-bearing blossoms has been noted by previous observers; but the paramount importance of blossom in their diet has never been appreciated. In fact, it may be said that only by becoming blossom feeders first and foremost has it been possible for them to build up and maintain their huge population in Australia. All the species of *Eucalyptus*, and a large number of the other trees of the "open" forest (which, as was stated above, is the dominant vegetation type in the coastal belt), provide heavy crops of blossom on which the fruit bats feed. The following is a list of the species which are known to be visited by the animals: Blue Gum (*Eucalyptus tereticornis*), Spotted Gum (*E. maculata*), Lemon-scented Gum (*E. citriodora*), White Gum (*E. alba*), Bloodwood (*E. corymbosa*), Blackbutt (*E. pilularis*), Ironbark (*E. paniculata* et spp. alia), Moreton Bay Ash (*E. tesselaris*), Box (*E. hemiphloia*), Stringybark (*E. acmenioides*?), a Messmate (*E. Cloeziana*), Woollybutt (*E. longifolia*), Apple (*Angophora subvelutina* and/or *intermedia*), Cabbage or Sugar Gum (*A. lanceolata*), Tea-trees (*Melaleuca* spp.), Turpentine (*Syncarpia laurifolia* and *Hillii*), Honeysuckle Oaks (*Banksia aemula* and *integrifolia*), Mistletoe (*Loranthus* spp.), and the Black Bean (*Castanospermum australe*—a rain-forest species).

These species are not all equally attractive. The most favoured seem to be Bloodwood, and the Spotted and Lemon-scented Gums (which are by some considered varieties of one species). The Ironbarks seem to be the least favoured, the silver-leaved variety (*E. melanophloia*) rarely, if ever, being visited. Bloodwood is perhaps the commonest and most widely distributed of the Eucalypts of the coastal belt. The Spotted Gum is also very common; and it is conceivable that its prevalence in certain districts, e.g. around Newcastle, New South Wales, may account for the apparently unusual density of the fruit bats in the locality.

Phot. 5. Swamp of Mangrove (*Rhizophora mucronata*) near Gladstone, Queensland. Site of a camp of *Pteropus gouldi*.

Phot. 6. Flight of *Pteropus scapulatus* over mangroves on Burnett River, Queensland.

Apart from blossom and cultivated fruit, native fruits, particularly of rain-forest trees, provide food for the bats. Chief among them are the wild figs, especially the Moreton Bay Fig (*Ficus macrophylla*), which is grown widely as a shade tree. As in the case of cultivated fruit, however, the importance of native fruits in the diet of the fruit bats has been exaggerated. Compared with the open (Eucalypt) forest association, the areas of rain forest in eastern Australia are almost insignificant, particularly in southern Queensland and New South Wales. (There are still considerable areas of rain forest along the border range; but, judging by my own observations and from reports received, fruit bats do not appear to be numerous there.) Whereas fruit bats derive food in the form of blossom from practically all the larger trees of the open forest, a minority only of the rain-forest species are a source of food in the form of edible fruit. Moreover, as the fruit of most rain-forest trees ripens in late autumn and winter, it is not generally available to fruit bats in New South Wales or southern Queensland, as they migrate from these parts in the winter months. The nightly congregation of great numbers of fruit bats in some tract of open forest, when a certain species of tree is in bloom, is a familiar phenomenon; but I could find little evidence of comparable activity in the case of rain-forest areas, except, to a lesser extent, when certain species of *Ficus* were bearing fruit. I have examined quantities of fruit scattered on the ground in the rain forest, but, with the exception of the fruit of a species of *Eugenia* in the north, I can recollect no instance when a fruit obviously bitten by bats was discovered. Thus the mere comparison of the areas of open forest and rain forest in eastern Australia clearly does not provide an adequate measure of the vastly greater importance of the former in the economy of the fruit-bat population.

V. THE FRUIT-BAT POPULATION.

(*a*) *The size of the population.*

Fruit bats being nocturnal, it is clear that a knowledge of the size and state of the population must be based on a study of the camps. The difficulty of obtaining estimates of numbers in the particular conditions in which the animals are found does not need to be emphasised (Pl. III, phot. 6). In the first place it is rarely possible to get a general view (or often even a general impression of the whole of a camp), unless, for instance, it is limited to a small mangrove-covered island, or an isolated "pocket" of rain forest. Thus it is very hard to get an accurate idea of its area. Then the density of the vegetation, and the restlessness of the bats themselves, render the actual counting no easy task.

From counts made in camps (of *Pt. poliocephalus*) it was found that a small tree carried about 100 individuals. The crown of such a tree would be equal in volume to a well-grown apple treee, some 12–15 ft. high. If the crowns of these trees (a small rain-forest tree is usually very tall and slender), were spaced as the trees in a typical orchard, at 20 ft. intervals, giving just over 100 trees to the acre, this would represent a density of 10,000 bats per acre. In

typical rain forest, however, there is a continuous canopy of foliage, and the animals hang in a zone which must sometimes be as much as 50 ft. in depth. It would therefore be safe to assume that, hanging in not abnormal density, the number of bats in a typical rain-forest camp would be twice this figure at least, i.e. 20,000 per acre. In a mangrove swamp, where the trees are rarely as much as 20 ft. high, the density would be less, probably nearer 10,000 per acre. Where *Pt. scapulatus* was concerned it would be greater, since this species tends to form more crowded camps than do the others, and moreover is fond of clustering in the lower growth, thus making better "use" of a given area of vegetation.

These figures provide a rough basis for calculating the number of individuals in a camp, once its approximate area is known. Needless to say, the result will be little more than an indication of the order of figures—thousands or tens of thousands—which can be used. The term "small" will be applied here to a camp covering half an acre or less (or a thinly inhabited camp of rather larger area), and thus would probably contain up to 5000–10,000 individuals; "medium-sized" up to 2 or 3 acres, containing up to 50,000; and "large" anything over this size.

Observations made in a camp near Rockhampton, in Queensland, indicate that these approximations are fairly accurate. The camp was considered large. In it the bats were distributed in a discontinuous way through some 5 to 10 acres of rain forest. There were considerable gaps between the groups of animals, and it was not often that a view of any large number could be obtained. The camp "broke" at precisely 6 p.m. (October 10th, 1929), first forming a packed wheeling mass above the trees, then moving off in a column about 100 yards wide and 100 ft. deep (in the centre). This column left the camp in almost undiminished intensity for a period of 25 min. I have timed fruit bats with a speedometer, and found that their speed of steady flight is about 25 m.p.h. Allowing an interval of 15 ft. in each direction between the individuals in the air, and the cross-section of the column to be one-half the rectangle 300 by 100 ft., this flight represents a number of about 200,000 bats.

Independent observations made by a correspondent at Esk, Queensland, also seem to confirm these estimates. He writes of a "large camp" which had been in the district for at least 20 years, and talks of it "diminishing to thirty or forty thousand." He has tried to estimate the evening flights, and on one occasion counted 32,000 bats passing over one point in about an hour. He points out that this would not represent the total of the camp, as more than one stream used to leave at nightfall.

During the investigation not many large camps were actually met with. Probably only two of those visited in New South Wales contained as many as 100,000 individuals; one in a Tea-tree swamp in the Nambucca State Forest (at least 50 per cent. *Pt. scapulatus*), the other near Kempsey. The latter completely filled a pocket of rain forest, 5–6 acres in area, and contained a small percentage of *Pt. scapulatus*.

The evidence collected indicated that the three larger species, *Pt. poliocephalus*, *gouldi* and *conspicillatus*, do not of themselves form really large camps as frequently as reports would lead one to believe. When a well-known camp of one or other of these species has been reported to attain unusual size, enquiries often discovered the fact that *Pt. scapulatus* was present as well. This species habitually forms large camps. (One on the Burnett River, Queensland, where Pl. III, phot. 6 was taken, was the largest camp met with. It covered over 10, possibly over 20 acres; and the animals were hanging so thickly that sixty were secured with six shots. It is probable that the numbers in this camp exceeded a quarter of a million, possibly considerably.) As *Pt. scapulatus* is found chiefly in north and central Queensland, it is natural that the biggest camps occur in these regions. Sometimes these northern camps attain an incredible size. The following statement was obtained from an informant living on the Gilbert River, in the Gulf country: "I heard one man who had been on the Red River say that in his opinion all the foxes[1] in the world were there. The camp was half a mile wide, and about four miles long, and they were there in millions." In this case the figure given appears to be literally correct. There is very little doubt that *Pt. scapulatus* was the species present in this case. Another report was received, also from north Queensland, of a camp, in this case *Pt. scapulatus* without doubt, which at times extended for "miles along a creek."

In southern Queensland, as in New South Wales, camps tend to be medium-sized or small, at any rate at the present time. Some, a few years ago (probably during heavy migrations of *Pt. scapulatus*), seem, however, to have rivalled the northern camps in size. Of two camps in the neighbourhood of Gympie, one is said to have covered 50 acres "in good years," the other 25.

Although certain camps are well known, the great majority are situated in unfrequented and often inaccessible spots. It would usually take many weeks to locate and visit all the camp sites in a given area, even an area of limited size. Even then there was no certainty that some site had not been overlooked. A survey of the whole of the animals' range being clearly out of the question, special attention had to be given to certain localities, selected on account of their importance either economically or in relation to the complex state of the mobile population.

In all forty-two camps were investigated, the great majority being in Queensland. Many were visited more than once, at different times of the year, in order to gain knowledge of the seasonal movements of the animals. As might be expected, with two or three exceptions only, these camps were of a "permanent" nature, i.e. inhabited annually, though perhaps for certain months of the year only, for it is rarely that the visit of an observer will coincide with the appearance in a district of a migrating mob of bats temporarily camped in a "new" site.

[1] Fruit bats in Australia are invariably known as "flying foxes."

In addition to the camps actually visited, information, by correspondence, etc., was collected of nearly 200 others. Many of these were purely temporary, and others, previously permanent, had been deserted of recent years. This figure, therefore, has little meaning (especially as very little of the information concerned northern Queensland), and so in order to get an idea of the numbers and distribution of camps it is necessary to generalise from the particular, that is from those districts in which the investigation was most thorough.

In the strip of country within 30 miles or so of the coast, immediately north of and including the estuary of the Burnett River, in Queensland, there are a number of camps with an average interval of less than 20 miles between them. All but one, so far as is known, are annually inhabited. Most in normal years are medium-sized, and in certain years are large.

In the Rockhampton district (central Queensland) the camps are even more closely spaced. In the area lying between the mouth of the Fitzroy River and Cario Creek (about 50 miles to the north), and extending about 30 miles inland, twelve camps were located. In addition it can safely be said that there would be one more at least near the mouth of the Fitzroy, which was not explored. Of these, eight are permanent or annual, seven being often large. Two were temporary camps of *Pt. scapulatus*, one being large. The remaining two were once permanent, but have dwindled to the point of disappearance during the last 3 or 4 years. This does not exhaust the total of the camps in this area in exceptional seasons. Information was received of at least four more sites which had been inhabited during the last few years.

Almost as close spacing of camps is found in the Townsville area, the Hinchinbrook area (from Ingham to Innisfail), and on the Atherton Tableland (all in north Queensland). In the last mentioned, in a rather limited area, five camps were located (three of which were visited), separated from one another by about 15 miles. Four of them are annually inhabited, and two at least are sometimes large.

Changes in the fruit-bat population of the more southern districts, due to increased settlement, etc. (see below), have taken place in recent years to a considerable extent, and thus it is difficult to get an accurate idea of the nature and distribution of camps at the present day. Three or four years ago, in south Queensland, there were at least nine annually inhabited camps between the New South Wales border and the Brisbane district, in an area some 70 miles long and 45 miles wide. Of late, one or two of these camps have been deserted, and others are no longer inhabited every year.

Still less can be said about New South Wales. Special attention was given to the Hunter Valley district, centred round Newcastle and Maitland. In the area, some 50 miles long, bounded by Morisset in the south and Port Stephens in the north, and extending as far inland as Cessnock, seven camp sites were located. Only two of them are definitely known to be annually inhabited, the camps in some years being large. One at least of the others was formerly in-

habited annually, but has lately only been inhabited at irregular intervals. This district is probably not typical of the New South Wales coast, as the Hunter Valley seems to act as a bottle-neck in the route of the southerly migration of the bats. Judging from the information available, it seems probable that along the New South Wales coast (with the exception of the closely-settled areas round Sydney) camps, now rarely large, are to be found at an average interval of rather under 40 miles.

The above sketchy survey indicates the great size of the fruit-bat population in eastern Australia; but it takes no account of the contributions of the different species in building up this population, or of the mass movements within it (for instance, one or two of the camps in the Rockhampton district referred to above are winter camps, occupied, presumably, by migrants from the south). This is inevitable, as much of the information, though checked as carefully as possible, was not obtained by personal observation.

(*b*) *The distribution and migrations of the species.*

The geographical ranges of the four species were given in brief at the beginning of the paper. These ranges are such that in no district can it safely be said that only one species of fruit bat will be found, unless it is the far inland areas into which *Pt. scapulatus* alone ventures.

Pt. scapulatus and *gouldi* have both been reported from Broome, north-western Australia, along the north coast of the continent, and from the islands off Cape York. They occur together down the coast as far as the Mary River. (A reliable report of a camp of *Pt. gouldi* in the mangroves of this estuary is the southernmost record of this species.) The western limit of *Pt. gouldi* is unknown.

Pt. scapulatus is a great wanderer, following the blooming of the Eucalypts and other trees. In this way it ranges very far afield. Southward it apparently reaches the Victorian border; and it has been reported, in Queensland, as far inland as Blackall, Longreach, Mitchell, and Dirranbandi. Its range is thus practically co-extensive with the sum of those of the other three Australian species.

Pt. conspicillatus, which also occurs in New Guinea, is only found in the coastal area of eastern north Queensland. Cardwell appears to be its southern limit. It was the only species actually observed on the Atherton Tableland, northern Queensland, though *Pt. scapulatus* undoubtedly occurs there in large numbers at times.

Pt. poliocephalus is found along the coast of New South Wales, occasionally in Victoria, and in south and central Queensland. During this investigation it was not found further north than the Rockhampton district. However, as there were one or two camps of this species in that area, it may be assumed to occur further north. (There are records (Anderson, 1912), of this species from Cape Upstart, near Bowen, and an unspecified locality in Cape York. I am of

opinion, however, that this species will not be found to-day very far north of Rockhampton.) A few regular camps of this species are found well over 100 miles from the coast in Queensland, e.g. near Eidsvold and Jandowae. In New South Wales, however, no annually inhabited camp of *Pt. poliocephalus* has ever been recorded as far inland as Tenterfield or Glen Innes.

The habit of regular, seasonal migration has been developed in three, at least, of the four species, to a greater or lesser extent. Information of a type from which an accurate picture of these movements could be built up was not procurable. Camps are rarely visited except by shooters; and few observers differentiate between the species. It was sometimes even impossible to discover whether or not a certain camp was inhabited for the whole of the year. It is likely, therefore, that the outline of the migrations given below may have to be modified in the light of fresh information.

Pt. poliocephalus carries out very regular seasonal migrations, moving southward in the spring into southern Queensland and New South Wales. The general nature of this movement can be followed by the occupation of the camps from north to south. In New South Wales the bats appear in the Northern Rivers (the coastal district just south of the border range), often in the early part of October. In the Hunter Valley they do not usually appear before the middle of November. In the south coast area I have no definite record of their appearance before the month of December.

The main migration into New South Wales seems to pass to the seaward of the border range (which runs east and west). Fruit bats are not common at points along the range itself. It seems probable that the bats which visit the northern tablelands in the fruit season (rarely arriving before the middle of December) have come from the coastal districts directly to the east, for they are regularly more numerous round Tenterfield than they are in the Stanthorpe district of Queensland, just over the border to the north. It is possible that the earlier arrivals, when they are of this species, represent a much smaller, direct migration into New South Wales by a more inland route. How small is this inland migration, if indeed it occurs at all, is indicated by the absence of any permanent camps of *Pt. poliocephalus* on the northern tableland.

It is not true to say that this species completely deserts the southern parts of its range during the winter months. It is said that isolated individuals can be seen at all times of the year. Moreover, in recent years at least, two large camps have been formed during the winter months in districts where fruit bats are usually summer visitors only. (Nambucca, New South Wales, 1928 and 1929; Allora, Queensland, 1929. Neither of these were formed in a recognised camping site.) It is possible that this represents a new departure in the habits of this species (see below).

In the southern districts of Queensland the camps are inhabited during the summer months only (approximately from October until May), as in New South Wales. From the Mary River northward, however, complications begin

to appear. At Tees, a few miles from Marlborough, a camp of *P. palumbus* is occupied annually for approximately the three months of April, May and June. A camp at Belle Tout, just north of Eastbourne, is usually occupied from February to June or July. In 1924 and 1925 it did not appear to until after the winter. The fact that the birds arrive as early as February seems to indicate that the camp is not formed of animals which have migrated from the south. Most of the *palumbus* camps between Eastbourne and Hailsham seem to be of this type.

North of Hailsham camps of two distinct types are found. Every winter camps of *P. palumbus* occur here and there, e.g. near Heron just north of Hailsham, and at Barnett near Bexhill-on-Sea. In addition there are camps which appear a few miles of these winter camps in which the species is found in mid summer and winter e.g. at Ringle, Brownbill and Brook all in the Bexhill-on-Sea district. Considerable scarcity data remains regarding the ultimate source of the late winter migrants in such large numbers from autumn (November and December) to the end of the season. Undoubtedly a more detailed survey of the the Bexhill-on-Sea district and probably the area lying further north, would discover additional winter camps of *P. palumbus*.

From the observed fact that there exist in the northern portion of their range camps in which *P. palumbus* occurs in mid summer and winter it is clear that the custom of southern migration is not uniform throughout the species. It is rather remarkable therefore, that this migration should be so well established and so regular. Certain camps in New South Wales have been known to have been occupied each autumn for some 30 years and it is said that birds can be expected to return a week the date of the last departure.

In addition to the major seasonal migration, there are smaller local movements apparently governed by the state of the food supply. Thus in the autumn and winter from the purely coastal strip of New South Wales e.g. Batemans, Jervis Bay, etc., and possibly the adjacent portion of Victoria, the species appears to depend to considerable extent on the fruit of the cabbage tree palm. On the other hand it has been noted in the Bexhill district, that when privet is a large permanent camp is formed, that the numbers appear to be greatest in wet years. As autumn or winter rain will usually be better over-all than the corresponding period in dry years, this fact would be in accordance with the observation. I admit it looks good, would not be generally applicable. The existence of camps which are permanently, but not annually occupied, is probably connected with these periodic local movements.

P. palumbus has not been recorded as making seasonal migrations. In the species does not move outside the tropical and sub-tropical zones, this is perhaps to be expected. Such movements as occur are probably connected with the availability of food supplies in the permanent territory. The impression gained during the investigation was that a considerable part of the

population left the coastal camps during the winter months. The enormous numbers that are in evidence in the mango season, and the complications due to the appearance of large numbers of *Pt. scapulatus* at times, probably helped to create an erroneous impression of the scarcity of *Pt. gouldi* during the winter months. This species was found camped on the Burnett River in May; and the fact that they attack citrus (which ripens in Queensland from April onwards) as far south as the Burnett area, seems to indicate that there is no general winter exodus from the southern portions of their range. There is no doubt, however, that there are considerable movements within the population, for camps constantly vary in size, and frequently break up for periods of a month or two at a time.

Pt. conspicillatus was only met with in the Cairns and Atherton districts in north Queensland, and sufficient observations could not be made to obtain an accurate idea of its migratory habits. There can be little doubt, however, that there is a seasonal movement from the Atherton Tableland at least (but not from the lowlands of the coast), for two of the camps visited there, and found to be inhabited in November, were deserted in July. One of these appeared to be a regular summer camp, being vacated from June to September annually. It is quite possible that the climatic conditions of this tableland, due to its altitude, render it unsuitable in the winter for a purely tropical species like *Pt. conspicillatus*.

The extensive migrations of *Pt. scapulatus* are almost certainly governed by the blossoming of the so-called hardwood trees; and as this is notoriously uncertain, the movements of this species show great irregularity. The biggest migrations of *Pt. scapulatus* are carried out independently of the other species. They are characterised by the size of the mobs concerned, and usually by the short periods spent in any one district—sometimes only a matter of days. I visited a patch of rain forest on the Atherton Tableland (which happened to contain a camp of *Pt. conspicillatus*), in which a horde of migrating *scapulatus* had camped for "a few days." It looked as though the place had been visited by a tornado. Trees were stripped of their leaves, and branches up to 9 in. or 1 ft. in diameter had been broken off by the weight of the animals.

These migrations, as was mentioned above, are by no means confined to the coastal belt. *Pt. scapulatus* is found in numbers west of the divide, from Pentland southward to Clermont and Springsure, and via the Dalby district to the Dumaresq River, and thus into New South Wales by a route considerably inland of that followed by *Pt. poliocephalus*.

When a district is already inhabited by another species of fruit bat, *Pt. scapulatus* will almost always use their camping sites. In fact, it is difficult to name a camp on the coast in which this species will not be found at suitable times. In the camp on Baffle Creek, which has been kept under observation for many years, *Pt. scapulatus* has been noticed in certain seasons. In 1930 they arrived in January (co-incidently with the flowering of the Bloodwood),

Phot. 8. Tea-tree (*Melaleuca*) swamp, New South Wales. Site of camp of *Pteropus poliocephalus* and *Pt. scapulatus*.

Phot. 7. Camp of *Pteropus poliocephalus* in Tea-tree swamp, northern New South Wales. Most of the bats had flown away when this photograph was taken.

Pt. poliocephalus not appearing until the end of February. *Scapulatus* left the camp in March, *poliocephalus* staying until July. How the migrants came to select this camp site, which was uninhabited at the time of their arrival, is a problem. Possibly they were guided to it by a few individuals of the larger species, which were noticed among them.

There is, of course, some sort of general order in the migrations of *Pt. scapulatus*, the main southerly movement taking place in the summer. In the north there are "pure" *scapulatus* camps which are regular enough, e.g. at Woodstock, near Townsville, in which the bats arrive some time in August or September each year, and leave regularly before the wet season (in the first week of November in 1930). In the winter months *Pt. scapulatus* is found in "countless numbers" in the far north (Gulf Rivers and Cape York[1]), feeding on the blossoms of Tea-trees (*Melaleuca* spp.).

The coastal migrations into New South Wales appear to be carried out in conjunction with *Pt. poliocephalus*, the two species regularly camping and feeding together. This migration varies greatly from year to year, being insignificant, possibly non-existent, in certain seasons. The great variation in the numbers of *Pt. scapulatus* is probably the chief factor in determining the severity of attacks on cultivated fruit, i.e. the good and bad "flying fox years," in New South Wales. It was hoped that it would be possible to discover the factors controlling the variations in the southerly migrations of *Pt. scapulatus*; but unfortunately the information of the migrations in past years is so scanty that the basis for any attempt at correlation, say with climatic periodicities, is unobtainable.

(*c*) *Changes in the population.*

Australia is still in a state in which settlement and clearing affect wider areas each year. The last two decades have seen the nature of the vegetation altered over considerable areas. It is only natural, therefore, that there should have been a noticeable change in the fruit-bat population over this period. From the evidence collected by means of questionnaires and personal enquiries (which is discussed in detail in the official report of the investigation (Ratcliffe, 1931)), it is clear that there has been a very marked decrease in the numbers of the animals, especially in southern Queensland and New South Wales. This has been brought about by the felling of rain forest (in which the bats sought shelter), and the "ring-barking" of large areas of open forest to increase its carrying capacity as pasture, and directly by the shooting of the bats *en masse*. As attacks on cultivated fruit have definitely been less severe during the period of the general decrease, it must be assumed that the effect of shooting (and probably more important, the continual disturbance of the camps in the breeding season, when most of the shoots take place) have kept

[1] **Thomson, D. F.**, unpublished report of visit to Cape York, 1928–9.

pace with the effect of the reduction (chiefly by "ring-barking") in the supply of "natural" food.

Apart from this "artificial" change (which has affected *Pt. poliocephalus* more than the other species), there is some indication that the fruit-bat population is undergoing a natural change. The distribution of the four Australian species rather points to a state of unstable equilibrium, suggesting very strongly a stage in a progressive colonisation. *Pt. conspicillatus* still "straddles" the Torres Straits, and occurs in south-eastern New Guinea, in the north-western districts of which it is replaced by *Pt. chrysauchen*, a very closely allied species. Presumably it was the last to invade the continent. *Pt. poliocephalus* and *scapulatus*, which alone have colonised the temperate zone in the south, are significantly more differentiated from their nearest relatives than are the other two Australian species, and were, probably, the earliest invaders.

It is hard to find evidence to show that the ranges of the species are still altering. It was mentioned above, however, that not many years ago *Pt. poliocephalus* was recorded as far north as the Cape York Peninsula. During the investigation, districts considerably south of this were fairly thoroughly surveyed, but this species was not found further north than Rockhampton. It looks, therefore, as though *Pt. poliocephalus* was being slowly pushed further southward by the competing *Pt. gouldi*.

If it is true that the range of *Pt. poliocephalus* is being gradually restricted in the north, it is natural to look for some compensating change in other directions. Its western limit has apparently been reached, and in the extreme south it is retreating before closer settlement. There remains, however, the possibility of its increasing its *winter* range. This could be achieved gradually, by limiting the northward migration in the autumn, or by means of a sudden experiment, a sort of "habit mutation" appearing in a section of the population. This rather unlikely possibility seems actually to have taken place. In 1928 a large mob of *Pt. poliocephalus* formed a camp in the Nambucca State Forest, New South Wales, and stayed there throughout that winter and the next. In 1929 another very large mob spent the winter in a mountain gulley near Allora, on the eastern edge of the Darling Downs, Queensland. This winter happened to be exceptionally cold, 12° of frost being recorded in this district. Although records of stragglers wintering in the south are common, the case of large camps doing this appears to be without precedent. (The fact that only young animals, almost certainly of the previous year's brood, and very old individuals, were shot in the Allora camp may be significant.)

During the investigation it was possible to collect evidence showing that *Pt. scapulatus* had in very recent years greatly increased the scope of its southerly migrations. This change occurred in the summer of 1926–7. It was mentioned above that this species migrates southward into New South Wales, partly in conjunction with *Pt. poliocephalus*, and partly independently: this

independent migration being more obvious in the inland areas, where the larger species rarely occurs. This inland migration has apparently not been regular, most of the districts on the western slopes of the northern tableland being visited "only at irregular intervals," or "every two or three years." The animals occurring occasionally at Coonabarabran and Gilgandra probably represent the advance guard of these inland migrations. The evidence that *Pt. scapulatus* is the only, or at any rate the principal, species concerned in this inland migration is largely indirect, for few of the reports from these areas differentiate between the species. A comparison with Queensland conditions, where *Pt. scapulatus* is undoubtedly the chief, if not the only inland wanderer, points to this conclusion. In the inland belt of New South Wales (i.e. the western slopes of the northern tableland), no "fixed" camps of *Pt. poliocephalus* are known. In the corresponding belt of southern Queensland such camps are widely scattered, and are diminishing in numbers. It is hardly conceivable, therefore, that large-scale migrations of *Pt. poliocephalus* could originate from this tract of country.

The coastal migration is largely obscured by the more obvious annual invasion of *Pt. poliocephalus*. As the two species are rarely distinguished, it was impossible to get an idea of its extent. There is no doubt, however, that it was well established prior to 1926, for informants in several districts were well acquainted with *Pt. scapulatus*, one knowing it in the Bega district, near the Victorian border, 30 years or more previously. The fact that so very few people realised the existence of a second species of fruit bat in New South Wales indicates that the migrations were rarely considerable. I am of opinion that *Pt. scapulatus* was, so to speak, carried along by the southerly migrating *Pt. poliocephalus*.

The summer of 1926–7 was quite exceptional. Generally throughout southern Queensland and New South Wales fruit bats were more in evidence than they had been for very many years, and losses to fruit growers were abnormally high. This state of affairs appears to have been directly caused by a quite exceptionally heavy migration of *Pt. scapulatus*. In southern Queensland its presence was noted in many *poliocephalus* camps, and in addition large mobs appeared here and there, forming temporary camps, often of great size, along the creeks. In New South Wales, *Pt. scapulatus* was specifically distinguished in at least three districts; for instance the Orchard Inspector at Windsor, near Sydney, definitely reporting that the fruit bats harrying the orchards in his district were "the small species, apparently from Queensland, which owing to drought conditions there migrated south." To anyone acquainted with the migrations of this species the conditions noted in New South Wales in 1926–7 were quite typical. In all the coastal districts fruit bats occurred in vast numbers, feeding on the flowering trees, and settling in sites not previously used as camps.

At the beginning of the investigation a questionnaire was circulated

throughout New South Wales asking for the dates when fruit bats were especially prevalent. In *almost every case* in which a specific date was mentioned, it was the summer of 1926–7. In one or two of the inland districts, e.g. the Murrumbidgee Irrigation Area, it was given as *the only year* in which fruit bats had ever been seen in those parts. Thus it is clear that the invasion, apart from being heavier than any previous migration, also extended further inland than any before.

This exceptional migration of *Pt. scapulatus* has proved of more than temporary importance, for it seems to some extent to have established the habit of *extensive* southerly migration into New South Wales. During the seasons 1927–8, 1929–30, and 1930–1, records of this species occurring in considerable numbers have been obtained from various districts in the State, e.g. the Hunter Valley, 1927–8; Nambucca and the northern tableland, 1929–30; Kurrajong, Kempsey, and the northern tableland, 1930–1. This change of habit is already having serious economic consequences, for *Pt. scapulatus*, in Queensland almost exclusively a blossom-eater, has readily taken to soft fruit in the coastal districts of New South Wales, particularly in the early part of the season. (This can probably be explained to some extent by the fact that the two species of *Eucalyptus* which are their chief source of food in many of these areas, i.e. *E. corymbosa* and *maculata*, do not blossom until well after Christmas.)

There can be little doubt that the cause of the unusual mass movement of 1926 must be sought in the very severe drought which was experienced over the greater part of Queensland in that year. Most severe, naturally, in the inland areas of the west and north-west, it even extended to the coastal districts as far south as the Mary River. It was surpassed in severity only by the great drought of 1902. As the greater part of the range of *Pt. scapulatus* in Queensland must have been affected, the blossom on which the bats depend probably failing completely in the drought-stricken areas, it is natural that an abnormal migration would result.

Whether the conditions which have obtained since 1926 will prove to be permanent, it is impossible to say. Droughts of equal severity have occurred in the past, and were presumably accompanied by widespread movements of *Pt. scapulatus* in search of alternative feeding areas. There seems to be no reason to suppose, for instance, that the effects of the drought of 1902 should have been radically different from those of the drought of 1926; but it has been impossible to discover whether heavy migrations of *Pt. scapulatus* occurred in the years immediately following. It is possible that other factors may have been at work in recent years (i.e. since 1926) which have helped to keep up the increased migrations of this species. A more effective colonisation of New South Wales would presumably be advantageous to the species, and would probably have been achieved gradually in any case, since the smaller migrations of past years have indicated that it was possible. However, it would seem that the migration as it is at present carried out was not biologically efficient.

This is indicated by the very severe attacks on cultivated fruit that have occurred in the early part of the season, e.g. in 1930 in the Sydney district, in the Hunter Valley (where green-stone fruit was attacked), and at Copeland a little further north (where citrus, usually immune, was eaten). Although these attacks on unripe fruit and citrus were undoubtedly the work of the larger *Pt. poliocephalus* (the weak dentition of *Pt. scapulatus* rendering such a feat virtually impossible), they indicate a general shortage of food which would be felt by both species alike. It is probable, therefore, that before the increased migration can be of real and permanent biological advantage to *Pt. scapulatus*, the time factor may have to be adjusted somewhat, which would largely neutralise the serious economic consequences of this change of habit.

VI. SUMMARY.

1. The Australian species of the genus *Pteropus* are described, and the probability that they colonised the continent from Austro-Malaya is discussed.

2. The nature of the vegetation found in the area concerned is briefly described.

3. The general and breeding habits of the four mainland species of fruit bat are described, and the differences in the breeding seasons noted. The problem of the natural control of numbers is discussed.

4. The diet of the animals is described, and the paramount importance of the blossom of the *Eucalyptus* forest species is emphasised.

5. An attempt is made to estimate the order of size of the fruit-bat population, based on the study of the size and distribution of the daytime "camps." The ranges of the four mainland species, and the nature and scope of their seasonal migrations are described. Evidence pointing to changes in the population due to settlement, and a natural expansion in the ranges of certain species, is discussed; and the recently increased migrations of one species (*Pt. scapulatus*) are specially noted.

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THE BIRD POPULATION ON AN OXFORDSHIRE FARM

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Part I. The winter population.

On March 10th, 1927, at the suggestion of Mr E. M. Nicholson, members of the Oxford Ornithological Society made a census of the birds present on part of the area of Temple Farm, Sandford-on-Thames, which was at that time the University Farm, but has since been sold. During the following winter counts of the birds on the same area were made four times, once each in October, December, January and February. In the winter of 1928–9 the only count was made in October.

During the two succeeding winters counts were made with greater regularity, seven in 1929–30 and twelve in 1930–31. Thus in five winters the birds on this area have been counted twenty-five times and it seems desirable to summarise the figures obtained, and to see what conclusions can be drawn from them.

The area included in the survey consists of three large and two small fields, all of them surrounded by hedges, together with a small wood adjacent to one of them, with a total area of 125 acres. The three large fields and one of the small ones are pastures used for grazing sheep and cows, but the remaining small field, called Short Corn, was stubble with clover at the outset. The lowest of the large fields, called Knapp's Ley, is very wet, containing a permanent pond which in wet weather sometimes extends over a considerable part of the grass. In this same field numerous small bushes of gorse and hawthorn had grown up during the period of University management, but have mostly been destroyed by burning since the farm passed into private hands.

The number of species of birds met with in this area on one or more occasions during the 5 years was fifty-one (or possibly fifty-two, if marsh and willow tits were both correctly identified), but only three species, viz. blackbird, chaffinch and robin, have been recorded on all twenty-five visits. Song thrush was present on twenty-four occasions, partridge and wren on twenty-three, starling and blue tit on twenty; whilst at the other end of the list corn bunting, cole tit, lesser spotted woodpecker, tawny owl and heron have each only been met with once.

The smallest number of individuals counted was 103 on February 19th, 1930, the largest 1018 on October 29th, 1930; whilst the average for the twenty-five counts was 290. The average numbers of individual species work out as follows: starling, 88; blackbird, 35; yellow hammer and wood pigeon, 17;

rook, 14; chaffinch and lapwing, 11; partridge, 9; song thrush and linnet, 8; robin and greenfinch, 7; blue tit, fieldfare and skylark, 6; meadow pipit, 5; redwing and goldfinch, 4; wren, long-tailed tit and stock dove, 3; hedge sparrow and great tit, 2; pheasant, green woodpecker, carrion crow, jay, snipe, house sparrow, bullfinch, marsh (or willow) tit, missel thrush, mallard and jackdaw, 1. The remaining seventeen species are too infrequent to have any average expressed by a whole number. It seems obvious that with a population which may fluctuate from 103 to 1018 a single count must be practically valueless. If then we compare the figures for the different winters, 1926–7 and 1928–9 must be omitted, since in each only one count was made. The averages for the total population in the other three seasons were: 1927–8 (four records), average 157 birds; 1929–30 (seven records), average 211 birds; 1930–1 (twelve records), average 400 birds. The great increase shown in the winter 1930–1 can be traced to the greater numbers of five species, the figures for which are as follows:

Average numbers of	1927–8	1929–30	1930–1
Starlings	7	56	146
Rooks	6	3	21
Lapwings	0	0	23
Wood pigeons	3	9	28
Yellow hammers	3	3	32

If the totals of these five species are subtracted from the annual totals we get: 1927–8, 157 − 19 = 138; 1929–30, 211 − 71 = 140; 1930–1, 400 − 250 = 150. At first sight it may seem an arbitrary proceeding to subtract the numbers for these five species, but actually there is some justification for it in the fact that these are the principal species which occur in flocks and feed largely on the ground in the fields, whilst the remaining species are mainly birds of the hedgerows. The increase in the numbers of starlings, rooks and lapwings in the last winter is almost certainly due to the constant presence in the fields throughout that winter of flocks of sheep and cows. Whether this also accounts for the increase of wood pigeons and yellow hammers seems more doubtful.

It has been mentioned that the largest number of birds counted on the area was 1018 on October 29th, 1930. On that date the census included 600 starlings, 100 rooks, 100 lapwings and 31 wood pigeons, so that if these flocks are subtracted we get 187 as the total of all other species on that day, a number not greatly larger than the average.

If now we consider the figures for each month we find that five counts were made in October, six in November, one in December, two in January, eight in February and three in March. The numbers of counts in December, January and March are hardly sufficient to give satisfactory averages so will be neglected. The averages for the three other months are as follows: October, 507; November, 306; February, 232. It is of course obvious that the resident population of any area must reach a maximum at the end of the breeding season and must then decline through the autumn and winter months to a minimum

at the beginning of the next breeding season, but in the case of such mobile creatures as birds this seasonal fluctuation may easily be obscured by migration. It would appear from the above figures that this is not the case in Oxfordshire. Not only the totals, but the figures for many individual species show a marked decline during the winter. The monthly averages for the eight species most commonly present on the area are as follows:

Average numbers in	Oct.	Nov.	Feb.
Blackbird	51	36	28
Chaffinch	21	15	4
Robin	10	8	7
Song thrush	11	8	8
Partridge	6	11	12
Wren	5	3	2
Starling	199	69	74
Blue tit	13	9	3

It will be seen that the partridge is the only one of these species which does not show a decrease.

The species previously referred to as occurring in flocks again show erratic numbers, and, as the starling is one of these, it is fairly clear that no great significance should be attached to the great apparent decline in its numbers between October and November.

If the totals for these five species (starling, rook, lapwing, wood pigeon and yellow hammer) are subtracted we have the following figures for the remaining species: October, 214; November, 177; February, 116. It will be seen that whilst the averages for each of three winters were approximately similar, when the flocking species were disregarded, those for the individual months still show a marked decline. It is concluded therefore that this decline, which we know must occur somewhere during the winter, does actually take place in Oxfordshire.

Mr C. Elton has suggested that it is not very satisfactory to deal with numbers of birds varying so greatly in size, and that this could be compensated for by using the weights of the birds. I am greatly indebted to the Rev. F. C. R. Jourdain for kindly extracting from a paper by Heinroth the weights in grammes of most of the species met with on the farm. The few which Heinroth does not give have been assigned weights on considerations of size. The following are a few of the weights which give some idea of the scale:

Heron	1500 g.	Blackbird	100 g.
Pheasant	900	Starling	77
Wood pigeon	500	Yellow hammer	30
Partridge	375	Great tit	18
Jackdaw	225	Goldcrest	5

It will be seen that on this scale 1 wood pigeon = 100 goldcrests and 1 pheasant = 50 great tits = 30 yellow hammers. Converting the numbers into weights on this basis I find that the average weight of birds on the area in October was 57·356 kg., in November 46·689 kg. and in February 32·161 kg. The decline during the winter is therefore still shown.

It has been mentioned that the area on which the census was taken was 125 acres and the average number of birds counted on twenty-five visits was 290, so that there are on the average between two and three birds per acre. It is doubtful if this figure is of any great importance, since most of the birds are in the hedges and the density probably depends much more on the mileage and thickness of these than on the acreage of the land between them.

PART II. THE SUMMER POPULATION.

In May and June of three different summers, those of 1927, 1930 and 1931, an attempt was made to ascertain the numbers of birds breeding or resident on the farm, including the part of it whose population in winter forms the subject of the first part of this paper. The method adopted varied in each season. In 1927 the birds themselves were marked on plans and several surveys made. When pairs or individual birds were found in the same locality on more than one occasion they were regarded as resident. In many instances the nests of resident pairs were actually located. In 1930 the survey was confined to nests and the population assumed to be double the number of nests found. In 1931 nests were located as far as possible, but birds were also noted. It had been intended to repeat the survey so as to eliminate birds which were not resident, but the constant succession of wet days prevented this.

In spite of these differences of method the results of the three summer surveys show very good agreement, and part of the difference which does exist can be attributed to the fact that in 1930 one of the small fields was omitted from the survey, whilst in 1931 the copse was not surveyed.

A more surprising fact is that the summer population appears to be almost identical in numbers with the winter one when the numbers for the birds which visit the area in flocks are omitted from the latter. (Similar visits of rooks, lapwings, etc. occur in summer, but the summer censuses dealt only with the birds apparently resident.)

The following are the totals:

Summer, 1927	147	Winter 1927–8	138
Summer, 1930	144	Winter, 1929–30	140
Summer, 1931	185	Winter, 1930–1	150
		Mean summer population	159
		Mean winter population	143

The agreement extends to a number of individual species:

	Summer mean	Winter mean
Blackbird	36	35
Robin	8	7
Song thrush	9	8
Wren	4	3
Linnet	8	7

Altogether forty-one species have been found on the area in one or other of the three summers, as against fifty-one species met with in winter at least once in the five years. Of these thirty-one species are common to the two lists.

*Bird Census of 125 acres at Sandford-on-Thames, Oxon.**

Species of bird	Winter population (October to March)																Summer population (May and June)			
	No. of times recorded	Greatest no. recorded	Least no. recorded	Average of 25 records	1926–7 (1 record)	1927–8 (4 records)	1928–9 (1 record)	1929–30 (7 records)	1930–1 (12 records)	Average of annual means	Oct. (5 records)	Nov. (6 records)	Dec. and Jan. (3 records)	Feb. (8 records)	March (3 records)	Average of monthly means	Mean of 3 previous averages	1927	1930	1931	Average of 3 summers
Blackbird (*Turdus merula*)	25	123	11	35	14	54	48	20	39	35	51	36	36	28	25	35	35	37	38	34	36
Chaffinch (*Fringilla coelebs*)	25	56	1	11	4	11	23	5	15	11	21	15	11	4	3	11	11	22	22	24	23
Robin (*Erithacus rubecula*)	25	17	2	7	3	4	12	4	10	7	10	8	5	7	5	7	7	16	–	7	8
Song thrush (*Turdus philomelos*)	24	18	0	8	3	7	14	4	12	8	11	8	9	8	3	8	8	8	8	11	9
Partridge (*Perdix perdix*)	23	26	0	9	4	2	12	15	6	8	6	11	5	12	3	8	8	2	–	2	1
Wren (*Troglodytes troglodytes*)	23	9	0	3	1	4	5	1	4	3	5	3	4	2	3	4	3	3	4	6	4
Starling (*Sturnus vulgaris*)	20	600	0	88	18	7	5	56	146	26	199	69	56	74	8	77	64	2	–	2	1
Blue tit (*Parus coeruleus*)	20	42	0	6	–	2	4	4	9	4	13	9	2	3	0	5	5	2	–	1	2
Hedge sparrow (*Prunella modularis*)	19	6	0	2	–	1	2	2	2	1	2	3	1	2	3	2	2	8	–	–	–
Yellow hammer (*Emberiza citrinella*)	18	88	0	17	5	3	4	3	32	9	8	5	11	21	53	18	15	7	–	4	4
Wood pigeon (*Columba palumbus*)	18	169	0	17	–	3	2	9	28	9	12	45	2	10	0	12	13	6	12	13	8
Greenfinch (*Chloris chloris*)	16	26	0	7	–	3	15	13	4	7	17	12	3	–	1	6	7	–	–	5	8
Great tit (*Parus major*)	15	13	0	2	–	1	1	3	2	1	3	2	1	2	1	2	2	–	–	2	1
Meadow pipit (*Anthus pratensis*)	14	34	0	5	1	2	34	3	5	9	10	8	4	1	0	4	6	2	–	–	1
Pheasant (*Phasianus colchicus*)	14	4	0	1	–	1	–	0	1	0	2	1	1	0	0	1	1	1	–	–	1
Green woodpecker (*Picus viridis*)	13	2	0	1	–	1	1	1	0	1	1	1	1	0	1	1	1	1	–	–	0
Linnet (*Carduelis cannabina*)	13	81	0	8	–	7	11	4	11	7	9	23	4	–	–	7	7	5	–	–	0
Rook (*Corvus frugilegus*)	12	100	0	14	68	6	2	3	21	20	24	9	3	9	33	13	16	–	2	2	2
Carrion crow (*Corvus corone*)	12	4	0	1	1	–	–	0	1	1	2	2	1	2	0	1	2	2	2	2	2
Jay (*Garrulus glandarius*)	11	4	0	1	–	1	4	0	1	1	2	1	1	0	0	1	1	2	4	–	–
Fieldfare (*Turdus pilaris*)	10	80	0	6	–	11	–	16	4	6	0	3	15	16	3	9	7	–	–	–	–
Long-tailed tit (*Aegithalos caudatus*)	10	24	0	3	–	–	–	4	4	2	5	3	3	5	–	3	3	2	–	2	1
Snipe (*Capella gallinago*)	10	3	0	1	–	–	–	0	1	0	–	0	2	2	–	1	1	–	–	–	–
Magpie (*Pica pica*)	10	2	0	0	–	0	2	0	0	1	1	0	–	1	0	0	0	–	–	–	–
Lapwing (*Vanellus vanellus*)	9	150	0	11	5	0	–	–	23	6	50	1	0	2	3	9	9	–	–	2	1

Tree creeper (*Certhia familiaris*)	9	2	0	0	–	1	–	0	–	0	1	–	1	1	–	1	0	–	–	–	–
Skylark (*Alauda arvensis*)	8	71	0	6	--	–	6	5	8	4	21	4	–	–	–	4	5	1	–	7	3
Redwing (*Turdus musicus*)	8	46	0	4	--	9	2	8	1	4	9	9	0	1	–	3	4	–	–	–	–
Goldfinch (*Carduelis carduelis*)	8	40	0	4	–	0	–	13	0	3	4	8	1	3	1	3	3	–	–	–	–
House sparrow (*Passer domesticus*)	8	15	0	1	7	0	2	3	1	3	2	3	–	0	3	1	2	3	–	2	2
Bullfinch (*Pyrrhula pyrrhula*)	8	5	0	1	–	0	–	1	1	0	1	2	–	–	1	1	1	–	2	–	1
Little owl (*Athene noctua*)	8	2	0	0	–	0	–	0	1	0	0	0	–	1	–	0	0	2	–	1	1
Kestrel (*Falco tinnunculus*)	8	1	0	0	–	0	1	0	0	0	0	1	0	–	0	0	0	2	–	–	1
Marsh (or willow) tit (*Parus palustris* or *P. atricapillus*)	7	6	0	1	–	1	1	–	1	1	0	0	1	1	–	1	1	–	2	–	1
Mistle thrush (*Turdus viscivorus*)	5	13	0	1	2	3	–	0	0	1	3	0	–	0	1	1	1	1	–	–	0
Mallard (*Anas platyrhynchos*)	5	6	0	1	–	1	–	1	0	0	–	–	–	2	–	0	0	–	–	–	–
Moorhen (*Gallinula chloropus*)	5	4	0	0	–	–	–	0	1	0	1	–	0	0	1	0	0	2	2	2	2
Stock dove (*Columba oenas*)	4	60	0	3	–	–	–	9	1	2	–	0	–	8	0	1	2	–	–	–	–
Stonechat (*Saxicola torquata*)	4	2	0	0	1	0	2	–	0	1	0	–	–	0	0	0	0	–	–	–	–
Goldcrest (*Regulus regulus*)	4	3	0	0	–	0	–	–	0	0	–	0	–	0	–	0	0	–	–	–	–
Jackdaw (*Coloeus monedula*)	3	13	0	1	1	–	–	–	1	0	–	0	–	2	0	0	0	–	–	–	–
Pied wagtail (*Motacilla alba*)	3	4	0	0	–	–	–	1	0	0	1	0	–	–	–	0	0	–	–	–	–
Barn owl (*Tyto alba*)	3	1	0	0	–	–	–	0	–	0	–	0	–	0	–	0	0	–	–	–	–
Tree sparrow (*Passer montanus*)	2	2	0	0	–	–	–	0	0	0	–	0	–	–	–	0	0	1	–	4	2
Reed bunting (*Emberiza schoeniclus*)	2	2	0	0	–	–	1	0	–	0	0	0	–	–	–	0	0	–	–	–	–
Sparrowhawk (*Accipiter nisus*)	2	1	0	0	–	–	–	0	–	0	–	0	–	0	–	0	0	–	–	–	–
Corn bunting (*Emberiza calandra*)	1	4	0	0	–	–	–	1	–	0	–	1	–	–	–	0	0	–	–	1	0
Cole tit (*Parus ater*)	1	1	0	0	–	0	–	–	–	0	–	–	0	–	–	0	0	–	–	–	–
Lesser spotted woodpecker (*Dryobates minor*)	1	1	0	0	–	0	–	–	–	0	–	–	–	0	–	0	0	–	–	–	–
Tawny owl (*Strix aluco*)	1	1	0	0	–	–	–	–	0	0	0	–	–	–	–	0	0	–	–	–	–
Heron (*Ardea cinerea*)	1	1	0	0	–	–	–	0	–	0	–	0	–	–	–	0	0	–	–	–	–
Whitethroat (*Sylvia communis*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	10	27	14
Whinchat (*Saxicola rubetra*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	4	2
Lesser whitethroat (*Sylvia curruca*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	4	2
Willow wren (*Phylloscopus trochilus*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	1	1
Sedge warbler (*Acrocephalus schoenobaenus*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	1
Tree pipit (*Anthus trivialis*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	1
Garden warbler (*Sylvia borin*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	1
Chiffchaff (*Phylloscopus collybita*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0
Spotted flycatcher (*Muscicapa striata*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0
Blackcap (*Sylvia atricapilla*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0
All species	25	1018	103	290	138	157	218	211	400	225	507	306	186	232	157	262	259	147	144	185	159

* The figures are given to the nearest whole number: 0 = average less than ½; – = entirely absent.

Of the twenty species met with in winter but not in summer only seven form an appreciable proportion of the winter population, viz. rook (winter mean 16), fieldfare (7), meadow pipit (6), redwing (4), goldfinch (3), stock dove (2) and snipe (1). Of these the fieldfare and redwing are, of course, winter migrants to England from more northerly regions, whilst the meadow pipit and snipe are mainly winter visitors in this part of England, only breeding in a few small areas of Oxfordshire.

The ten species found in summer but not in winter are all summer migrants to England from more southerly lands. The seven which form an appreciable proportion of the summer population of this area are whitethroat (summer mean 14), lesser whitethroat (2), whinchat (2), willow wren (1), sedge warbler (1), garden warbler (1) and tree pipit (1).

Detailed figures for summer and winter for each species will be found in the attached table. In conclusion I must record my indebtedness to Mr V. C. Wynne Edwards, whose manuscript report on the census of 1927 has been utilised in this paper, and especially to Mr J. D. Wood, Secretary of the Oxford Ornithological Society, for reports on the summer censuses of 1930 and 1931, and for valuable help in compiling the figures of the winter censuses. To him and to previous secretaries of the Society, and to a large number of its members, is due the credit for continuing somewhat monotonous surveys over a period of 5 years in the hope that some facts of interest would result.

Summary.

Census work on 125 acres of farm land near Oxford, carried out over several years, showed that the number of birds on the area decreased throughout the winter months. This decrease was also shown by the total weights of birds on the area, and represents the dying or departure of the surplus birds produced in the previous summer. The average number of birds was two to three per acre.

NOTES ON THE RELATIONSHIP OF SOME COMMON BIRDS OF N.E. MARAJÓ (N. BRAZIL) TO THEIR ENVIRONMENT

By J. T. CUNNINGHAM, M.A., F.L.S.

and D. M. REID (*Department of Biology, Harrow School.*)

(*With one Figure in the Text.*)

The following notes were made while on an expedition (financed by the Trustees of the Percy Sladen Memorial Fund and the Royal Society) to the island of Marajó. The island, which is about the size of Wales, lies in the mouth of the Amazon and within a few miles of the equator. The climate is of the wet and dry season type with a maximum temperature in the shade of about 90° F. This low figure is due to the strong trade winds which blow over the island.

The country is of an almost uniform flatness only slightly raised above sea-level. On this account it is intersected by numerous water channels called "igarapés" which resemble canals much more than rivers except that they are tidal. Of course, this does not mean that they contain salt water.

Although Marajó is in the Tropical Forest Belt it is distinguished by its great area of campo land which is given over to the grazing of cattle. The forest occurs only as strips or great clumps called "Ilhas de Matto." These Ilhas may be one of two types; if they occur on the open campo some distance from water they are free from undergrowth, so that one may walk through them with but little inconvenience. If, however, they occur near water, e.g. along an igarapé, they are impenetrable.

The campo may also be divided for our present purpose into two convenient types, viz. the long grass and the short grass campo. These also may be correlated with the water supply, the latter in the drier parts, the former in the wetter. This latter again passes almost imperceptibly into the permanent swamps.

During the dry season (August to February) this grass, excepting of course that of the permanent swamps, is burned dry and brown, while in the height of the wet season the whole land may be covered with 2 to 3 ft. of water.

On the north coast the land is rather lower than on the east and south, and since that coast is more exposed to the floods of the main river, it tends to be more heavily flooded during the wet season. This, however, has its compensations because it does not suffer to the same extent through desiccation during the dry season. For the same reason the Ilhas de Matto in this region are more dense than those in the south and east.

The regular swamps are to be found at the head of the igarapés where the tides overflow into depressions on the campo, so that these swamps are caused

and kept up not so much by the inability of water to drain out as by its actual pouring in.

It is necessary to make a few brief remarks about the characteristic vegetation of each of these areas.

A. Forest (Ilha de Matto):

(*a*) Dry type. Tucumá (*Astrocaryum tucuma* Mart.); Bacabá (*Oenocarpus* sp.); Babassú (*Orbignia speciosa*) and other palms and many deciduous trees.

(*b*) Wet type. Mangrove (*Rhizophora* sp.); Assahí (*Entrepe precatoria*); Bamboo. Fewer palms generally. Many deciduous trees, e.g. Tapiribá (*Spondias lutea*). Where this type fringes permanent water, e.g. an igarapé, there is often a thin line of Aninga (*Montrichardia arborescens*) growing in the water.

B. Campo:

(*a*) Dry type. Short grasses.

(*b*) Wet type. Long grasses.

(*c*) Water (swamp). Aninga and *Papyrus*.

Each of these three localities forms a definite food-type area and in consequence will tend to have a definite bird fauna. This is complicated by the fact that there appears to be a considerable amount of movement from one area to another because of various intervening factors. Thus, birds may feed on the campo and shelter in the forest, etc. Each area, however, tends to provide a typical food—the forest provides fruit and soft leaves, the campo provides grass seeds and insects, while the water provides fish and aquatic organisms generally.

The movements of the birds may best be illustrated by the diagram (Fig. 1). The birds definitely confined to the localities *A*, *B*, *C* and *E* are of relatively few species. The greatest number of species are to be found in *D* and *F*.

The typical forest birds (*A*) are generally poor fliers but have beaks strong enough to deal with hard fruits (such as the parrots) or, like the woodpeckers, to pierce the tree trunks in search of grubs.

The only really typical campo birds are two: (1) the spur-winged plover (*Belonopterus cayannensis*) and (2) the meadow pipit (*Anthus lutescens*). Some, but not all, of the ducks are typical of the water habitat, but the "Pato de Matto" (*Cairina moschata*) finds shelter in the forest. The waders are confined to the edges of the shallow waters.

In the following list the common name as well as the scientific one is given. In using the former we have adhered, as far as possible, to the English form (e.g. scarlet ibis instead of Guará).

The classification and nomenclature is that used by Dr E. Snethlage in the *Catalogo das Aves Amazonicas*, 1914.

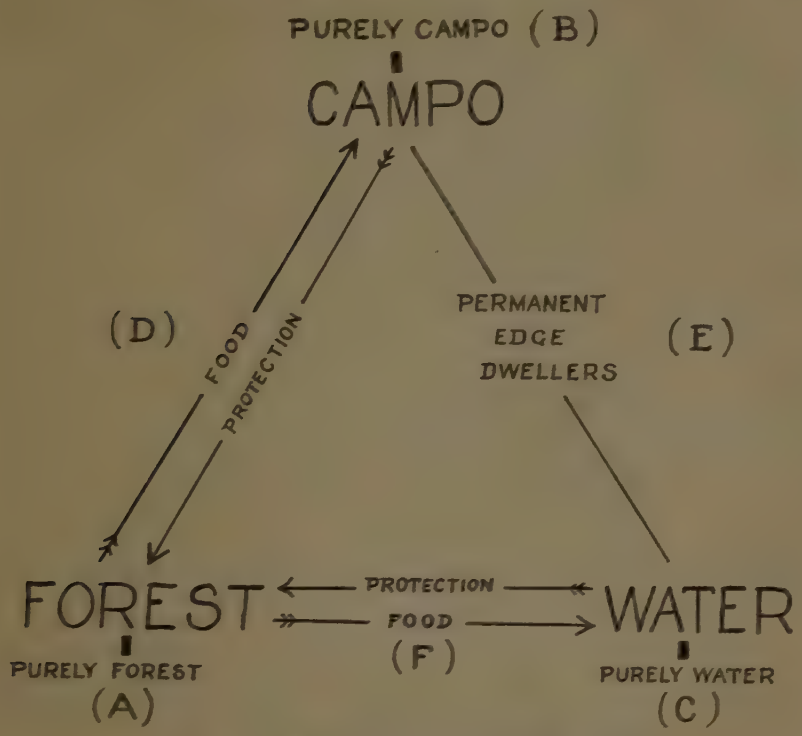

Fig. 1. The letters in brackets refer to the lists of Birds.

List of birds with their habitat.

A. *Forest.*

Common name	Scientific name	Remarks
Cigana	Opisthocomus hoazin (Müll.)	Largely confined to the bamboos. It is not eaten by the natives because of the unpleasant taste of its flesh
Gavião	Leucopternis superciliaris Pelz.	
Parroquet	Conurus aureus (Gm.)	Very fond of seed of sensitive mimosa
Green parrot	Pionus menstruus (Linn.)	Roosts in a definite place and travels fair distances to feed
Toucan	Rhamphastos toco Müll.	
Toucan	Pteroglossus araçari (L.)	
Woodpecker	Campophilus rubicollis (Bodd.)	
Tree-creeper	Glyphorynchus cuneatus (Licht.)	
Wren	Troglodytes musculus clarus Beryl & Hart.	
Caraxué	Dendrocincla phaeochroa B. & H.	
Rouxinol	Icterus cayannensis (L.)	
Gallo da Campina	Paroaria gularis (L.)	Feeds on the ground beneath the trees and on the campo edge
Tesoura	Milvulus tyrannus (L.)	Confined to the trees of the campo edge and feeds on insects in the air

B. *Campo.*

Common name	Scientific name	Remarks
Spur-wing plover	Belonopterus cayannensis (Gm.)	
Curicáca	Theristicus caudatus (Bodd.)	
Nightjar	Podagar nacunda (Vieill.)	Sometimes found in the more open forests
Small nightjar	Caprimulgus nigrescens Cab.	
Meadow pipit	Anthus lutescens Puch.	
Baieta	Leistes militaris (L.)	
Blue swallow	Tachycineta albiventer (Bodd.)	
Perdiz	Rhynchotus rufescens catingae Reisr.	

C. *Water.*

Marreca cabloco	Dendrocycna discolor Sclater	Occur in vast flocks up to several thousands
M. ananhy	Nettion braziliense (Gm.)	on the treeless water channels

D. *Campo and forest.*

Pomba galega	Columba rufina Temm.	
Pomba de bando	Zenaida iessieae Ridg.	
Black-headed Urubú	Cathartes urubutinga Pelz.	
Red-headed Urubú	C. aura pernigra (Sharpe)	
Egret	Herodius egretta (Wils.)	Feeds also in swampy places
Maguarý	Ardea cocoi L.	
Groló	Crotophaga major Gm.	Found also in long grass in swampy places
Quirirú	Guira guira (Gm.)	
Maria e Dia	Empidomonus varius (Vieill.)	
Cabeça branca	Arundinicola leucocephala (L.)	
Japyim	Cacicus cela (L.)	
Lavandeira	Taenioptera velata (Licht.)	
Japocaní	Donacobius atricapillus (L.)	
Iratauá	Gymnomystax mexicanus (L.)	

E. *Water at campo edge.*

Massarico	Charadrius dominicus (Müll.)	Mostly confined to water channels in open
Massarico	Aegialitis collaris (Vieill.)	campo, rarely on tree-lined igarapés
Jaçana	Parra iacana L.	

F. *Forest and water.*

Tayazú	Nycticorax nycticorax naevius (Bodd.)	
Roseate spoonbill	Ajaja ajaja (L.)	
Scarlet ibis	Eudocimus ruber (L.)	Mostly occur in flocks
Pato do Matto	Cairina moschata (L.)	
Mergulhão	Phalarocorax vigua (Vieill.)	
Carara	Plotus anhinga L.	
Kingfisher (large)	Ceryle torquata (L.)	
Kingfisher (small)	C. inda (L.)	

TERRITORY AMONG WOOD ANTS (*FORMICA RUFA* L.) AT PICKET HILL

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(*With Plate V and one Figure in the Text.*)

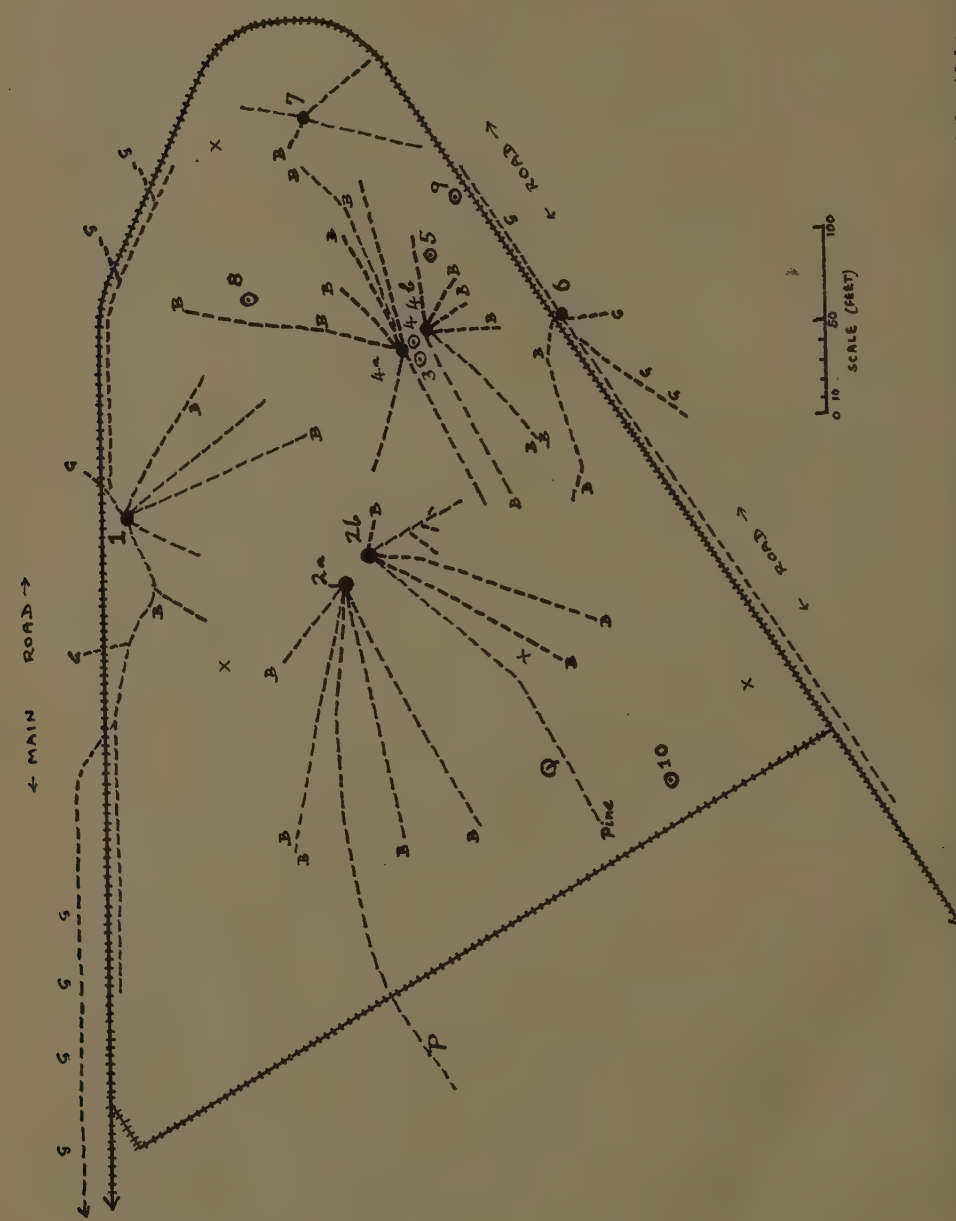
Introduction.

The sketch-map (Text-fig. 1) shows the distribution in July, 1929, of the nests and trackways of the wood ants living in Dr T. G. Longstaff's bird sanctuary at Picket Hill on the edge of the New Forest near Ringwood, Hampshire. The ants were studied at irregular intervals between 1927 and 1929 during visits to Dr and Mrs Longstaff, to whom I owe a debt of thanks for hospitality, encouragement, and help in planning the survey.

The wood ants lived only at one end of the garden, where a complex area of heather (*Calluna vulgaris*), birch (*Betula alba*), sallow (*Salix caprea*), oak (*Quercus robur*), and other plants, intersected by turfy paths and forming in places a dense undergrowth, has been kept for some years as a bird sanctuary (Longstaff, 1926). The ants were destroyed by the owner in 1930, owing to their repressive effect on the nesting birds. This can be seen in the sketch-map on which are marked the positions of the nests of willow wrens, whose nestlings are certainly liable to attack by ants (Longstaff, 1927), which have been observed elsewhere to keep away birds from pine trees (Hudson, 1923). The ants were named by Mr O. W. Richards, and the aphids by Mr F. Laing, to both of whom, and to Prof. E. B. Poulton, F.R.S., my thanks are due.

Densities of population.

What little is known about the actual populations of ant nests has been summarised by Andrews (1929), who shows that the size of the nest does not necessarily give an indication of the number of ants inhabiting it, and that various estimates and counts of the nests of *Formica rufa* in different countries range from 5000 to 100,000 per nest. He concludes that a figure of at least 10,000 is probably not uncommon. Much further work is needed, but it seems at any rate permissible to state that the nests of *F. rufa* are comparable with country towns in England as regards the size of their populations; an average urban town is about 50,000. This would be the same as a large ant nest. Taking the present map (Text-fig. 1) as an example (though not necessarily a typical example) of a community of ant nests, and comparing it with a small-scale



Text-fig. 1. Sketch-map July 20th, 1929, of wood ant trackways and nests in bird sanctuary at Picket Hill. *Black dots* are nests; *circles with dots* are places of former nests; *broken lines* are trackways; *barred lines* are fences or hedges; some, but not all, birch trees are put in (*B*), including majority visited by ants. Track from nest 1 outside the hedge continued 100 ft. further west among gorse bushes (*G*). Approximate positions of willow wren nests in 1929 are shown by four crosses.

Ordnance Survey map of southern England, it appears that the nests and trackway systems of the ants are, on a linear scale, about a thousand times smaller than those of man. Ökland (1930) gives the dry weight of *Formica rufa* as about 2 mg. when not carrying food. The human body is about two-thirds water, so that the average dry weight of a human being will be roughly 13,000 gm. The relative weights of a wood ant and an average human being are therefore very roughly one to six million, and it would appear that the superiority in weights of population per acre occupied may not be very much greater in man. The actual areas covered by the two species are of course very different. We are able to see here the importance of clearly defining what is meant by density of population. There is in the first place the *Lowest Density*, which is the number of animals divided by the total area covered by the census. There is secondly the *Economic Density*, which is the number of animals divided into the area of territory which they actually visit or live in, and which supplies their food. There is thirdly the *Greatest Density*, which includes all local (often temporary) aggregations within the territory. With the wood ants the *Lowest Density* (*LD*) would be, say, the number of *F. rufa* per acre in Hampshire, which would be a very low figure. The *Economic Density* (*ED*) would be the number of *F. rufa* per acre of the ground actually covered by their nesting territories in Picket Hill sanctuary. The *Greatest Density* (*GD*) would be the number in the nest at night, or the number in the closely packed groups that sit sluggishly about on the surface of the nest in early spring. *LD* is the usual measure taken in such work as bird censuses, although it is admitted by ornithologists that many species may in fact feed in only a limited part of the area studied. It gives some measure of the biological success of a species over a comparatively large tract of country comprising many smaller habitat variations, but depends also on the results of competing plant species and the distribution of basic geographical factors. *ED* will often tend to be a constant density even in a fluctuating population, since increases in *ED* will usually lead to migration into empty areas until a limiting figure is reached. In some cases this will be the same as *LD*. *GD* is of importance in animal aggregations of the type studied by Allee (1931) and others, and of particular importance in relation to the spread of diseases and parasites. The limit here is actual contact between the individuals. The distinction between these different types of population density is of some importance. A further step is the elimination of size differences by the determination of weights as well as numbers of individuals. To do this a large amount of data not usually available are required, e.g. the age distribution, weights at different ages, etc. By combining these weight data, and the census data, it would be possible to compare the actual biological success of a species much more easily. Thus, as has been suggested above, the *Economic Density* of wood ants at Picket Hill, in terms of weights per acre, may not be very widely different from that of man. This hypothesis requires testing by further work in determining the real *Economic Density* both

of ants and of man, and does not allow for the rural population which has been treated in this comparison as if it fulfilled the same rôle for the townsmen as aphids on trees and shrubs do for the ants.

When we make such comparisons it has of course to be remembered that the ants are cold-blooded organisms working only at maximum efficiency in the summer months, whereas man has to maintain his body at a high temperature throughout the year, so that his total biochemical turnover in a year is much greater. Population studies should ultimately be developed to a point where such turnover, now expressed in crude ecological terms can be put into physiological or biochemical terms. We need, finally, to know the total areas to which each of these densities refers, and the time during which they operate.

Trackways.

The wood ants at Picket Hill appeared to live mainly by the farming of aphids on trees and shrubs, especially on birches. Trackways led from each nest to these trees, which appeared to determine the shape and extent of the territories of each nest. The trackways shown on the map vary in length from 8 to 80 yards, and are usually straight. In one instance the ants had adopted the same curved path as man (nest 1, an old nest, which was certainly in existence as far back as 1913). In two others (*P* and *Q*) fresh extensions of trackways were curved or bent. It is probable that the final straight route is attained when such new extensions become permanently established. This explanation does not account for the curve in the track of nest 1. This nest also had another peculiarity, found fully developed only in it and in nest 6: many of the trackways had definite forks. During the daytime in summer swarms of ants could be seen hurrying to and from the nest along all these trackways. Where the turf paths were crossed the grass was killed and showed a brown line. Some of the paths remained the same during the three years of observation, i.e. the same trees were used. Others were observed to change both in length and direction, as fresh exploring parties invaded new territories or young trees grew up.

Farming habits.

Aphids occurred in large numbers on the birch trees visited by the ants. Each group of aphids (which sit on the bark of the twigs) was usually guarded by one or more ants which assumed a threatening attitude when anyone approached near. Meanwhile other ants made continual journeys, at any rate during the day. Very few ants were ever seen carrying any preys along these trackways, and in fact practically no insects occurred on the birch-tree "farms," no doubt owing to the swarms of ants which destroyed them. The aphids formed therefore almost pure cultures on the trees, analogous to the flocks of sheep that are protected by man not only from enemies such as wolves, but also from competitors such as rabbits, and in the same way that cats are eliminated by the owner of this bird sanctuary. In the last week of March,

Phot. 1. General view in early summer of bird sanctuary where the ant nests occurred, with young birches, sallow, broom, heather, bramble, and grasses. Nests 2*a* and 2*b* occur here, but cannot be seen in the photograph.

Phot. 2. Nest 9. Small size shown by foot-ruler in front. Photo. taken August, 1927. Nest almost destroyed by green woodpecker between August and September, 1928. Seen rebuilding at end of March, 1929. Raided and mostly destroyed by ants from nest 6 on March 31st, 1929. No signs of nest in July, 1929.

1929, some observations were made upon the flow of the sap in the birches. At this time practically no aphids were to be seen on the trees, and very few ants. There was a great flow of sap in the birches on which the buds were not yet bursting. If the twigs were broken the water dripped out, tasting pleasant and sweetish. Some twigs were broken in the morning, and by the evening about fifteen ants were clustered round the running sap. Next day there were twenty-two ants. This flow of sap was observed to stop in the evening.

Aphids are simply employed to obtain the sap that the ants are normally unable to get directly. Aphid farms were also found on brooms (*Cytisus scoparius*), gorse (*Ulex europaeus*), occasionally on hawthorn (*Crataegus* sp.), and probably on oaks (*Quercus robur*).[1] Nests 1 and 6 were supplied by two long outer hedges of the sanctuary, in which were some large oaks and birches, and by the gorse which occurred abundantly outside the garden. They never crossed the main road on the north side. The ants from nests 2*a*, 2*b*, 4*a* and 4*b* mainly visited birches, also brooms. These differences were presumably accidental and due to the situations of the nests, but it is interesting to note the resulting differences in the type of trackways and the shape of their territories. Raiding, i.e. indiscriminate killing and collecting of insects and other small animals, was occasionally noticed, and may have been practised at seasons when I was not there, but aphid farming predominated in the summer months.

NEST TERRITORIES.

There was no connection between the trackways of neighbouring nests, i.e. the community of seven nests was divided into seven distinct units which worked with independent food territories, trees, and tracks. In some instances there was a neutral zone between the edges of the territories (e.g. between nest 4*b* and nest 6, and between nest 2*a* and nest 1). Ants from one trackway were transferred to a trackway belonging to another nest and their behaviour watched. They were not attacked, though sometimes touched by the antennae of the other ants, but appeared to be lost and unable to find their way, while the other ants were hurrying very definitely back and forth. The reciprocal experiment was tried with similar results. It is to be concluded that there is not normally any hostility between nests, neither are there common tracks or food supply. The territories surrounding two old nests (nests 8 and 10) that had died out some time before 1927 were still partly unoccupied in 1929, either through being unsuitable, or through the conservative habits of the other ants. Nest 10 used to depend on the only large pine tree in the garden; owing to the possibility of the wood ants spreading further towards the house, Dr Longstaff some years ago tied tarred cloth round the base of the tree, and this apparently caused the dying out of the nest, since visits to the tree were no longer possible. This tree was unoccupied in 1927 and 1928, but in 1929 the

[1] Aphids: *Symydobius oblongus* (Heyd.) on birch; *Aphis rumicis*, L. on broom and gorse; *Thelaxes dryophila* (Schrank) on oak.

newly divided nest 2*b* had sent out a very long column which occupied the tree. Ants were not commonly seen on the sallows and this may account for the territory of the deserted nest 8 not being occupied, since sallows had grown up thickly here.

A little more light is thrown on the territory system of the ants by a raid which was witnessed on March 31st, 1929. The spring was rather late, and there were still practically no aphids on the birches. Foraging parties of ants appeared to be carrying home very few preys. At this time nest 6 sent out a party of ants which was seen to attack and destroy the population of the small nest 9 shown in Pl. V, phot. 2. The ants were being killed and carried back (no live ants were found in the jaws of the attackers). This small nest lay on the boundary of two larger territories, and had a relatively small territory of its own, e.g. a trackway from nest 7 came to a birch tree within 6 ft. of nest 9. There were no signs of nest 9 in the summer of 1929, and it would appear that its destruction was almost entirely due to the raid in March, though green woodpeckers (*Picus viridis*) may have finished it off. It seems probable that this sudden war took place at a time of temporary famine, though this is a theory difficult to prove.

Splitting of nests.

Some observations were made on the origin of the two nests 4*a* and 4*b*. In 1927 there was only one big nest (3). The ants moved from here to a spot several yards away, after they had been disturbed by the cutting of a new path through the undergrowth. The new large nest (4) was present in the spring of 1928, when it was seen to give off two subsidiary nests. On April 9th, most of the nests in the sanctuary were still rather inactive. In the first warmth of spring the ants come up and sit about sluggishly on or near the nests in dense masses. This phase lasts several days, after which normal activities, in which building is prominent, begin. These spring aggregations are very striking, and their significance is not understood. On the 9th there were two new nests being built about 6–10 ft. away on opposite sides of the old one. One at least was along a permanent trackway, though these were not yet in active occupation. These two nests were the future 4*a* and 4*b*. There was at first very active communication between the young growing nests and the old one. The 6 ft. separating 4*a* from the parent nest swarmed with ants running both ways, mostly carrying nothing. Those that did carry anything had building material, occasionally preys, and also commonly *live* ants, and sometimes injured and dead ants. The main nest was obviously more than half deserted, though the ants still left were building busily. Nest 4*a* had also sent out a foraging party eastwards. By April 11th practically all communication had ceased between 4*a* and 4, but 4*b* was now reaching full activity and ants could now be seen actively carrying to and from the main nest, many with live ones in their jaws. These living ants were carried both ways. This splitting of the old nest

was not permanent, for by September of 1928 both new subsidiary nests had died out, while the old one was occupied and flourishing. Observations by Dr Longstaff and myself make it probable that the new nests were destroyed by woodpeckers.

In the spring of 1929 (March 31st) exactly the same splitting process was seen in action, the two new nests (at exactly the same spots as before), being built up very vigorously, while the parent nest this time was almost completely deserted and inactive. Digging revealed a good many ants, but they were nearly all smaller than the others, and appeared to have no social stimulus to build. Some of these ants were placed with some ants from nest 4*a* on a piece of brown paper. There was great activity and some of the larger 4*a* ants ran up and felt the others with their antennae, and several times picked them up and then dropped them again. There was no sign of hostility. Yet at this time there was no communication at all between the parent nest and the young ones, in spite of the large amount of apparently suitable building material available on the big one. A trail of small piles of this material was placed between nest 4*a* and the old nest (a distance of about 6 ft.), but only the nearer half of the line was visited from nest 4*a*, whose ants collected some of the material. There appeared to be a definite, and to human perceptions invisible, barrier separating the two nests. This could not be explained by any active defence from the old nest, nor by the distance, since at this time nest 4*a* had a foraging party as far as 50 ft. away along the same line as the previous year. This year, the two new nests grew in size and successfully established themselves, splitting between them the territory and trackways of the original nest (see Text-fig. 1).

Many curious features remain to be elucidated. The general account just given has been made objectively true so far as possible, though no doubt many points have been missed. The facts show, at any rate, that *Formica rufa* can form new nests without either a marriage flight or the social parasitism of *Formica fusca* described in Donisthorpe (1927). The latter will probably be found to be the method employed in long-distance dispersal; it is curious that the ants have never adopted the splitting process in moving to greater distances, e.g. the other end of the garden, or across the main road, where ample suitable habitats exist. Nests 2*a* and 2*b* probably arose in the same way, by splitting. When the first attempts were made to destroy the ants by putting paraffin on the nests, the remnants of the population scattered and founded new units along the old trackway systems. A similar scattering and splitting into small nests was seen to have taken place in Tubney Woods, Berkshire, where in one place *F. rufa* had lived under an old tree stump. The tree stump had been uprooted, and at the time of the visit there were as many as seven little nests in the neighbourhood of the old one and arranged in a manner suggesting an old trackway system (the ants in these woods also tend aphids on birches, sycamores, and other trees).

Enemies.

The chief enemy besides man and the occasional armies of other nests, is the green woodpecker (*Picus viridis*) which was often seen digging into the nests, and probably was responsible for the partial or complete destruction of nests 5, 7 and 9 in 1928. No other birds are known to attack the wood ants regularly at Picket Hill; but on August 14th, 1926, a migrating pied flycatcher (*Muscicapa hypoleuca*) (shot for identification) was found to have its crop crammed with *Formica rufa* (T. G. Longstaff).

Summary.

1. A survey was made of the nests and trackways of an isolated community of wood ants (*Formica rufa*) in a bird sanctuary in Hampshire.

2. Each nest had a distinct territory containing certain trees and shrubs on which lived almost pure cultures of aphids tended by the ants for their secretions, and forming the basis of trackway systems from the nests.

3. There was no communication between the trackways of neighbouring nests, nor normally any hostility between ants of different nests, except for occasional destructive raids.

4. One nest was observed to split into two, which then divided up between them the original territory and had no further communication.

5. The main check on numbers of the wood ants was the green woodpecker (*Picus viridis*).

6. The different methods of working out densities in numbers of animal populations are discussed in relation to wood ants and to man.

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A STUDY OF THE PREY OF *DIOCTRIA RUFIPES* DE G. (DIPTERA, ASILIDAE) IN AN OXFORD COMMUNITY

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Previous papers on the prey of Asilid flies have usually dealt with material collected sporadically in various localities over a period of years. The scope of this paper is limited to the investigation of a single community in the University Parks, Oxford, during the early part of June, 1931. All the material is preserved in the Hope Department, University Museum, Oxford, where the work has been carried on under the direction of Prof. E. B. Poulton, D.Sc., F.R.S., to whom my best thanks are due for much kind help and advice. I desire also to acknowledge my indebtedness to Messrs R. B. Benson, J. E. Collin, A. H. Hamm, W. F. Johnson, G. Nixon, A. W. Stelfox and Commander J. J. Walker, without whose kind assistance in identification the work could never have been completed.

The nature of the prey caught by predacious insects is limited by many interacting and overlapping factors of which the four following are apparently of prime importance: (1) morphology; (2) the method of hunting; (3) the ecological association in which the insect lives; (4) preferential selection.

With regard to the first of these Melin (1923) has pointed out that the proboscis of *Dioctria rufipes* has a strong upturned hypopharynx, possibly specially adapted for the piercing of hard chitin. At least half the prey recorded in this paper are species with a hard integument (e.g. Hymenoptera, Coleoptera, Asilidae). Again, the legs of *Dioctria* have only a scanty covering of hair, but although small insects would therefore appear difficult to retain, the prey includes a few small species such as *Phora*, *Oscinis* and *Opius*.

Considering the second of the above factors, it must be noted that *D. rufipes* hunts its prey from both high and low points of vantage, usually seizing it by means of "capture-darts" but occasionally seeking it in the course of longer flights. The single Lepidopterous larva recorded as prey may either have been picked off the vegetation in flight, or, as is more likely, taken while hanging suspended by a silken thread, in the course of a "capture-dart." Although the Asilids were sometimes noticed at rest on trees, at a height of about 8 ft. from the ground, attention was entirely confined to those found among low herbage.

Under the third heading, that of ecological associations, is included the relative abundance in the community of insects other than the *Dioctria*. That this abundance is reflected in the prey of *D. rufipes* is clearly shown by the data given below. This Asilid occurred most commonly among long meadow

grass and on and about clumps of nettles and umbelliferous flowers, in situations usually, but not always, near the shelter of trees (cf. Melin, 1923, p. 23, fig. 18). The dominant species of Diptera in the locality appeared to be the Bibionid *Dilophus femoratus* Mg. (very abundant on umbelliferous flowers and occurred six times as prey); *Empis trigramma* Mg. (very common among nettles and other low herbage and occurred fourteen times as prey); and the Asilids *Dioctria rufipes* De G. (four times as prey) and *Dioctria atricapilla* Mg. (twice as prey). The remaining Dipterous prey included five Syrphidae, four Anthomyidae, and a few specimens of several other families

There can be no doubt that *Dioctria* exercises preferential selection. This conclusion is of especial interest since no such strongly supported evidence for this factor is as yet available for any other genus among the British Asilidae. A quarter of the prey were Ichneumonidae, twelve species, mostly represented by single specimens, being among the captures observed. *Pycnocryptus peregrinator* L., probably the most abundant Ichneumonid in the locality, was represented by eight examples. It must furthermore be emphasised that the large proportion of Ichneumonid prey cannot be explained by the abundance of these insects, for although Hymenoptera doubtless occurred in considerable numbers they were certainly not so conspicuous as to become a dominant group in the community. A similar preponderance of Ichneumonid prey has been recorded in previously published accounts of *Dioctria*, and is most probably due to an incipient specialisation in habits comparable to, but not as yet so complete as, that found in other groups, e.g. Crabronidae. Furthermore a comparison with the prey of other genera proves that *Dioctria* is the chief among the Asilid foes of the Ichneumonidae (Poulton, 1906; Hobby, 1930)—a conclusion of considerable economic importance. Other Hymenopterous prey included four Braconidae (once), one Proctotrypidae, seven Tenthredinidae and one Aculeate. Three Coleoptera complete the list.

Although eighty-eight specimens of forty-nine species representing four orders were observed as prey it is very remarkable that only one of these (*Syritta pipiens* L.) should have been previously recorded as food of this Asilid (cf. Hobby, 1930). In the following table two orders and ten families of which no members have hitherto been recorded as prey of *D. rufipes* are indicated by means of an asterisk.

Poulton (1906) showed that female Asilidae are more often taken with prey than are males, a result confirmed by Hobby (1930) and in the present paper (57 ♀♀, 31 ♂♂). This difference between the predatory habits of the sexes has doubtless been brought about by the necessity for ripening the ova.

Poulton's observations also suggest that in certain species of Asilidae females with prey might be specially sought by the males. Careful attention to this point failed to reveal any such relationship between courtship and predacious habits in *Dioctria* (Hobby, 1931*a*).

Table of the prey of Dioctria rufipes De G. All from the University Parks, Oxford, June 1931.

Serial no. and sex of captor	Prey	Date	Remarks
	*Lepidoptera (1 = 1·1 %),		
1. ♂	Small larva, sp. indet.	11. vi. 31	Capture of Lepidopterous larva by Asilid is almost unique; cf. instance recorded by Carpenter (1931).
	*Coleoptera (3 = 3·4 %),		
	*Staphylinidae		
2. ♂	*Tachyporus nitidulus* L.	12. vi. 31	
3. ♂	*Tachyporus hypnorum* F.	8. vi. 31	
	*Silphidae		
4. ♂	*Corpse quercus* Gyll., ♂	9. vi. 31	
	Hymenoptera (35 = 39·8 %),		
	Braconidae		
5. ♀	*Bassus pictus* Nees., ♀	11. vi. 31	Apparently rare in Britain.
6. ♂	*Braon* sp. indet., ♂	12. vi. 31	
7. ♂	*Microgaster fuscicornis* Wesm., ♂	"	
8. ♂	*Opius crepitans* Wesm., ♂	8. vi. 31	
	Ichneumonidae		
9. ♀	*Exeristes* sp. ? *maculatus* Grav., ♀	4. vi. 31	"There is some doubt of this as I have no specimens to compare it with, and the lower mandibular tooth is longer than the upper." —A.W.S.
10. ♂	*Hemiteles fasciatus* Grav., ♂	12. vi. 31	Captured by K. P. Armstrong
11. ♂	*Ichneumon intactor* F., ♂	8. vi. 31	
12. ♂	*Mesoleptus ultimatus* Holmgr., ♂	10. vi. 31	
13. ♂	*Microcryptus* sp. indet., ♂	8. vi. 31	
14. ♂	*Ophion luteus* (Linnaeus) Gmel., ♂	10. vi. 31	
15. ♂	*Phygadeuon* sp. indet., ♂	8. vi. 31	
16. ♂	*Pimpla examinator* F., ♂	"	"Sent by Morley as variety of *P. turionellae* L." —A.W.S.
17. ♂	*Platycryptus perspicillator* Grav., ♂	17. vi. 31	"Specimen small but cannot, I think, be any other species." —A.W.S.
18. ♀	*Promethes pulchellus* Holmgr., ♀	12. vi. 31	Captured by K. P. Armstrong
19. ♂	*Pycnocryptus perspicuator* L., ♀	4. vi. 31	All specimens of this species are females
20. ♀	" " " "	8. vi. 31	
21. ♀	" " " "	"	
22. ♀	" " " "	"	
23. ♀	" " " "	11. vi. 31	
24. ♀	" " " "	"	
25. ♀	" " " "	12. vi. 31	Asilid captor courted by male
26. ♀	" " " "	"	
27. ♂	*Tryphon signator* Grav., ♂	4. vi. 31	
28. ♀	" " " "	12. vi. 31	
29. ♀	" " " "	"	
30. ♀	" " " "	"	

* Orders and families of which no members have hitherto been recorded as prey of *D. rufipes*.

Serial no. and sex of captor	Prey	Date	Remarks
	*Proctotrypidae		
31. ♂	*Phaenoserphus viator* Hal., ♂	15. vi. 31	
	Tenthredinidae		
32. ♂	*Enura atra* Jur., ♀	4. vi. 31	
33. ♀	*Selandria serva* F., ♀	12. vi. 31	
34. ♀	,, ,, ,, ♂	,,	
35. ♀	*Tenthredopsis nassata* L., ♀	4. vi. 31	
36. ♀	,, ,, ,, ,,	,,	
37. ♀	,, ,, ,, ,,	,,	
38. ♀	Sp. indet.	8. vi. 31	
	Andrenidae		
39. ♀	*Andrena minutula* Kirb., ♀	12. vi. 31	Asilid captor courted by male
	Diptera (49 = 55·7 %)		
	Nematocera		
40. ♂	*Fam. & sp. indet.	12. vi. 31	
	Bibionidae		
41. ♀	*Bibio hortulanus* L., ♂	12. vi. 31	
42. ♀	*Dilophus femoratus* Mg., ♂	4. vi. 31	Specimens of this species nearly all males
43. ♂	,, ,, ,, ,,	,,	
44. ♀	,, ,, ,, ,,	,,	
45. ♀	,, ,, ,, ,,	8. vi. 31	
46. ♀	,, ,, ,, ,,	,,	
47. ♂	,, ,, ,, ♀	,,	
	Stratiomyidae		
48. ♂	*Beris clavipes* L., ♀	12. vi. 31	Captured by K. F. Armstrong
49. ♀	,, ,, ,, ,,	,,	Asilid captor courted by male
	*Leptidae		
50. ♀	*Leptis tringaria* F., ♂	8. vi. 31	
	*Asilidae		
51. ♀	*Dioctria atricapilla* Mg., ♂	12. vi. 31	
52. ♀	,, ,, ,, ,,	,,	
53. ♀	*Dioctria rufipes* De G., ♀	4. vi. 31	
54. ♀	,, ,, ,, ♂	8. vi. 31	
55. ♀	,, ,, ,, ,,	12. vi. 31	
56. ♀	,, ,, ,, ,,	,,	
	Empididae		
57. ♀	*Empis brevicornis* Lw., ♀	11. vi. 31	
58. ♂	*Empis caudatula* Lw., ♀	4. vi. 31	
59. ♀	*Empis trigramma* Mg., ♀	,,	Only one male of this species captured
60. ♀	,, ,, ,, ,,	,,	
61. ♂	,, ,, ,, ,,	,,	
62. ♀	,, ,, ,, ,,	,,	Asilid captor courted by male
63. ♀	,, ,, ,, ♂	,,	
64. ♀	,, ,, ,, ♀	8. vi. 31	
65. ♀	,, ,, ,, ,,	,,	
66. ♂	,, ,, ,, ,,	,,	
67. ♀	,, ,, ,, sex indet.	,,	
68. ♀	,, ,, ,, ♀	11. vi. 31	
69. ♀	,, ,, ,, ,,	12. vi. 31	
70. ♀	,, ,, ,, sex indet.	,,	
71. ♂	,, ,, ,, ♀	,,	

Serial no. and sex of captor	Prey	Date	Remarks
	Syrphidae		
72. ♀	*Melanostoma scalare* F., ♀	4. vi. 31	
73. ♂	*Platychirus albimanus* F., ♂	8. vi. 31	
74. ♂	„ „ „ „	12. vi. 31	
75. ♂	*Syritta pipiens* L., ♂	8. vi. 31	Only species previously recorded as prey of *D. rufipes*
76. ♂	„ „ „ ♀	„	
	Anthomyidae		
77. ♀	*Egle dissecta* Mg., ♂	12. vi. 31	
78. ♀	*Hylephila personata* Collin, ♀	8. vi. 31	
79. ♀	„ „ „ „	12. vi. 31	
80. ♀	*Phorbia curvicauda* Zett., ♀	4. vi. 31	
	Cordyluridae		
81. ♂	*Norellia spinimana* Fall., ♀	8. vi. 31	
	*Psilidae		
82. ♀	*Psila fimetaria* L., ♀	8. vi. 31	
83. ♂	*Psila nigricornis* Mg., ♀	4. vi. 31	
	*Ortalidae		
84. ♀	*Dorycera gramina* F., ♀	8. vi. 31	
	*Chloropidae		
85. ♂	*Oscinis frit* L., ♀	12. vi. 31	
	*Phoridae		
86. ♂	*Phora* (*Chaetoneurophora*) *unispinosa* Zett., ♀	8. vi. 31	
87. ♀	*Phora* sp. indet. (*concinna* group), ♀	„	
88. ♀	„ „ „ ♂	12. vi. 31	

Species previously recorded as prey of Dioctria rufipes *De G.* (*Hobby*, 1930).

HEMIPTERA: ‡Capsidae.—†*Miris calcaratus* Fall.

HYMENOPTERA: Tenthredinidae.—†*Ametastegia glabrata* Fall.; †*Blenocampa assimilis* Fall.; †*Dineura stilata* Klug. Ichneumonidae.—†*Angitia* sp.? *interrupta* Holmgr.; †*Barichneumon semirufus* Grav., or *bimaculatus* Grav.; *Cratocryptus* sp.; *Hypamblys transfuga* Thoms.; *Hypomecus quadrimaculatus*; *Ischnus nigricollis* Westm.; *Microcryptus basizonius* [Grav.]; †*Pimpla oculatoria* F.; †*Pimpla* sp. ? *detrita* Holmgr., or *calobata* Grav. Braconidae.—*Alysia* sp., †*Bracon* sp. Andrenidae.—*Sphecodes* sp.

DIPTERA. Bibionidae.—†*Bibio pomonae* F. ‡Tipulidae.—†*Tipula oleracea* L. Stratiomyidae.—†*Chloromyia formosa* Scop. Empididae.—†*Empis pennipes* L. Syrphidae.—†*Sphegina clunipes* Fall.; †*Syritta pipiens* L. Anthomyidae.—†*Musca domestica* L. Cordyluridae.—†*Paralleloma albipes* Fall., †*Scatophaga stercoraria* F. ‡Sphaeroceridae.—†*Copromyza equina* Fall.

† Recorded from England, remainder from other European countries.

‡ Families not recorded in the present paper.

SUMMARY.

1. Female Asilids were more often taken with prey than were males (57 ♀♀, 31 ♂♂).

2. No relationship between courtship and predacious habits was detected.

3. Forty-nine species (mainly Diptera and Hymenoptera) were observed as prey; only one of these has been previously recorded as food of this Asilid.

4. The prey included a few small species but was, on the whole, of medium size.

5. The prey included many species with a hard integument.

6. The relative abundance of other insects in the community was reflected in the prey taken.

7. Preferential selection of Ichneumonid prey was exercised.

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NOTES

THE NUMBERS OF THE GREAT GREY SEAL (*HALICHOERUS GRYPUS*) ON ST KILDA AND NORTH RONA.

Little is known of the annual status of the great grey or Atlantic seal, for it frequents the more remote islands of northern Scotland. From July 22nd until August 14th, 1931, I was on St Kilda, and during that time was able to visit all the islands of the group, and obtain a fairly accurate estimate of the numbers of this species. The figures obtained were as follows: Hirta, 20 (mostly single); Dun, 30 (caves on south side); Boreray, 90 (east and north sides); Soay, 110 (chiefly south-east end). Total about 250 seals. The scarcity of seals on Hirta, the main island of the group, is surprising in view of the abundance of suitable caves and cliff areas; perhaps the evacuation of the islanders in 1930 will lead to an increase.

From August 28th until September 3rd, 1931, I was on North Rona, and during this time made as careful an estimate as possible of the seal population, as follows: south side, 30 (Pol Thothatom); south-west peninsula, 30; west side, 70 (most in two big caves); north end, 80 (in small groups); east side, 10; south-east rocks, 40. Total about 260 seals. A single individual also noted 8 miles south-east of Rona on August 28th.

Considering the available coastline in each case, seals are relatively far more abundant on Rona; this is not surprising, for the island has been uninhabited since 1844. Nevertheless parties from Lewis made annual visits for the seals, as recorded by Harvie-Brown (*Proc. Roy. Phys. Soc. Edinburgh*, 1835–8, pp. 288–9), in one of the very few papers on the fauna of this remote island. John Morris reported that 107 skins were taken in 1883, 143 in 1884, and 89 in 1885; J. N. Anderson (of Stornoway), estimated the annual killing prior to 1890 at between 120 and 150 individuals. Incidentally, it is noticeable that in autumn this species tends to form separate communities of from fifteen to twenty individuals, with considerable distances often separating each group.

T. H. HARRISSON.

A NERVOUS DISEASE AMONG FOXES.

During the early autumn of 1916 or 1917 I observed three examples of a kind of madness among foxes, apparently due to some nervous disease affecting the brain. The locality was the borders of Oxfordshire and Berkshire, 5–6 miles south of Oxford. The first case was that of a vixen which was seen repeatedly to rush headlong at a fence composed of iron bars; after each dash it would return into the field, sit down, and snap viciously at the air, then dash at the fence again with the result that its nose became very much cut and bruised.

The same fox was known to return to this spot and go through the same manœuvres on several different days. On one of these occasions the fox was shot, and upon opening the skull small hæmorrhages were found upon the surface of the left side of the brain. No other lesions or signs of injury, apart from the shot wounds, were found in any part of the body. In the second case, a vixen was seen to behave in an exactly similar manner by rushing at a wire-netting fence around an orchard; this occurred on several occasions, the fox being quite oblivious to the presence of human beings while thus engaged. When killed, it was found to have similar lesions on the left side of the brain. The third case, a dog fox, was seen by several observers to behave in a remarkable manner: in broad daylight it would run about the fields, taking no notice of human beings. On one occasion it was seen by some workmen running round in circles, snapping at the air, and appeared quite unaware of their shouts and efforts to drive it away. When I first observed this fox it was running across a field towards me, stopping occasionally to snap and behave in the same hysterical manner; finally it ran headlong into a small dew-pond in the middle of the field and was drowned. Upon examination this fox was found to have brain lesions identical with those of the first two cases, and in addition a large quantity of pus was present between the top of the skull and the brain. Otherwise the animal appeared to be in perfect condition, and in this case there was no risk of confusing shot wounds with pathological symptoms as the fox was not shot; the lungs were full of water, showing that death must have taken place through drowning when the animal plunged into the dew-pond.

GEORGE TICKNER.

SYPHILIS AS A DISEASE OF WILD RABBITS AND HARES.

During the past few years several instances of syphilitic infections among rabbits and hares in Great Britain have come to my notice, and in most cases I have been able to confirm the existence of this disease by demonstrating the presence of a spirochaete (presumably *Treponema cuniculi*) under the dark-ground microscope. In East Yorkshire a disease having all the outward symptoms of syphilis was common in 1907 and 1925 among hares, and was said to be the cause of considerable mortality among these animals. In the East Harling district of Norfolk rabbits were frequently found to be covered with fungus-like scabs, and a specimen which I examined in 1929 showed *Treponema* to be numerous in the tissues underlying the external scabs. In this district it was stated that rabbit trappers became afflicted with painful sores on the hands and arms after handling the diseased rabbits. In the Leadenham district of Lincolnshire hares showing the same symptoms have been observed during the past 10 years, and an examination showed the same spirochaetal infection. Other rabbits examined and found to be infected with *Treponema* were from Laverstoke, Hampshire, and Dolphinton, Peebles, in 1931, while

evidence of the existence of the disease among rabbits in South Lincolnshire and Stirlingshire, and among hares in North Oxfordshire, was obtained from eyewitnesses but not confirmed by microscopic examination.

This disease of rabbits and hares, though first described by Ross (1912) and Bayon (1913), seems to have received very little attention from the epidemiological point of view, especially in so far as it concerns wild rabbit and hare populations, and its apparently widespread existence in this country makes this neglect rather surprising. The external symptoms are very obvious, though the unskilled observer may occasionally diagnose them as a form of sarcoptic mange; the head, inner sides of fore- and hind-legs, and the genitalia, are the most frequent sites of infection, though scabs may occur practically anywhere on the body in a badly affected animal. These scabs are hard, grey, and granular, and slightly raised, and their appearance has not unnaturally caused them to be attributed to the growth of a fungus on superficial examination. The spirochetes are numerous in the tissues immediately underneath these excrudescences, and are easily seen under a $\frac{1}{12}$th in. oil immersion with dark-ground illumination, when they appear exactly similar to the organisms of human syphilis (*Treponema pallidum*). *Treponema cuniculi* has, however, been proved to be non-pathogenic to human beings, and shows a negative reaction to the Wassermann test.

In its occurrence among wild rabbits and hares this disease shows a peculiarly local distribution, often being found to be present among the rabbits in one warren or hedgerow, while numerous other colonies of rabbits in the same district remain completely free from it. The mode of spread is presumably by contact, especially during coitus, but ticks, fleas, and lice may well play an active part in transmitting the disease from one animal to another. All the diseased specimens I have examined have been adults.

A. D. MIDDLETON.

NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

1. GENERAL PAPERS ON PARTICULAR GROUPS OF ANIMALS.

1. Goffe, E. R. "British Tabanidae (Diptera)." *Trans. Ent. Soc. South England*, **1930**, 43–114. 1931.

2. ECOLOGICAL SURVEYS AND HABITAT NOTES.

(*a*) Marine.

See also **11, 22.**

2. Lowndes, A. G. "*Eurytemora thompsoni* A. Willey: a New European Record." *Nature*, **128**, 967. 1931.

This copepod was found in a brackish pool in Sussex. Hitherto only known from Nova Scotia (in a fish stomach), and in the brackish water of the Sea of Okhotsk. (Comment on this record by R. Gurney, *Nature*, **129**, 98, 1932, together with citations of similar discontinuous records of the distribution of copepod species.) A full description of the species, the pool in which it occurred and its animal associates, is given by Lowndes in *Ann. and Mag. Nat. Hist.* **8**, 501–7. 1931.

(*b*) Freshwater.

See also **7.**

3. Lowndes, A. G. "Some Fresh-water Entomostraca of the Birmingham District." *Ann. and Mag. Nat. Hist.* **8**, 561–77. 1931.

A list of 99 species is recorded, and descriptions of certain rare ostracods are included (one, *Iliocypris ambigua*, being a new species). The copepod *Eurytemora velox*, normally a brackish water inhabitant, was found in a reservoir in company with *Diaptomus gracilis* and other species. *D. gracilis* was found in five other pieces of water in which *Eurytemora* was not found. Lists of species for different zones and habitats are given. Notes on the distribution of the large cladoceran *Leptodora kindtii* are given, also on the seasonal occurrence of *Cyclops strenuus*.

(*c*) Land.

See also **28, 32, 33, 34.**

4. Bristowe, W. S. "The Spiders of the Orkney and Shetland Islands." *Proc. Zool. Soc. London*, 951–6. 1931.

Lists of spiders, with discussion on their distribution elsewhere. Ants are scarce on these islands, and it is suggested that the unusual abundance of woodlice, earwigs and carabid beetles was due to this cause.

5. Bristowe, W. S. "A Contribution to the Knowledge of the Spiders of South Wales." *Ann. and Mag. Nat. Hist.* **8**, 173–7. 1931.

Height data and other habitat notes for certain localities in Brecknock, Carmarthen, Monmouthshire and Pembrokeshire. Two phalangids and one false scorpion are included.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS.

See also **32, 35, 36.**

6. Moe, A. "The North Sea as a Link between Climate, Plant Growth and Migration in the British Isles and in Norway. Spring near Yarmouth and at Stavanger." *Quart. Journ. Roy. Meteorological Soc.* **57**, 35–42. 1931.

The author points out the similarity in climate of these localities, due to the common influence of the warm Atlantic current, and gives records (Norfolk, from the Marsham diaries covering 200 years; and Stavanger 1917–25) showing a close similarity in the dates of flowering of certain plants, and the arrival of certain spring migrants. The resemblance is shown closely by average dates, and quite well by the variations from year to year in actual dates. The validity of averaging the dates of flowering of different species is discussed, and the author concludes that this process gives a better phenological index of local climate than the species taken separately.

7. Butcher, R. W., Pentelow, F. T. K. and **Woodley, J. W. A.** "An Investigation of the River Lark and the Effect of Beet Sugar Pollution." *Min. of Agr. and Fish. Fishery Investigations*, Ser. 1, **8**, No. 3, 1–112. 1931. (H.M. Stationery Office. 6*s.* net.)

An important biological survey of a small river in East Anglia. Plant associations are described in relation to environmental factors and seasonal pollution. They appeared to suffer less from factory effluents than the animals. Beet-sugar factory effluents were present only in the winter, and gave rise for several years to extensive winter growths of "sewage fungus" over many miles. This growth consisted mainly of fungus, *Sphaerotilus natans* and allied species, but sometimes contained the colonial protozoan *Carchesium spectabile*. The growth hindered fishing by getting on lines, was unpleasant in other ways, and the lowered oxygen content of the water occasionally killed fish, and probably caused migration in most winters. The animal inhabitants of different bottom habitats and plant associations are listed. The chief effect of the effluent was to increase the numbers of mud-bottom animals and decrease the number of gravel-bottom forms. This was caused by silting. The exact effects on fish food were not ascertained. The work on invertebrates was done quantitatively, and a new type of digger dredge is described, also other methods. After several years of experiment, purification plant was installed which appeared to prevent the pollution of the river. The authors emphasise the general lack of biological survey data for lowland rivers in England.

8. Bristowe, W. S. "Notes on the Biology of Spiders. 4. Further notes on Aquatic Spiders...." *Ann. and Mag. Nat. Hist.* **8**, 457–65. 1931.

Observations were made on a common terrestrial species, *Lycosa pullata*, which also frequents intertidal mud flats in search of prey. It retreats to land when the tide comes up. Experiments showed that its direction of movement was related to the slope of the shore, and not to vision, etc.

9. Sikes, E. K. "Notes on Breeding Fleas, with Reference to Humidity and Feeding." *Parasitology*, **23**, 243–9. 1931.

Experiments on the grey squirrel flea, *Ceratophyllus wickhami*, proved that the optimum relative humidity of air for the larval development was about 80 per cent., and that 15–28 per cent. of moisture in the food gave good results. Dried mammalian blood was found to be a successful diet for the larvae.

10. Robson, G. C. "The Adaptability of the Molluscan Classes." *Proc. Malacological Soc.* **19**, 259–66. 1931.

A review of the relations of molluscan structures to their environment, with especial reference to the manner in which these limit the general ecological distribution of the molluscan classes.

11. Pantin, C. F. A. "The Adaptation of *Gunda ulvae* to Salinity. 1. The Environment." *Journ. Exp. Biol.* **8**, 63–72. 1931.

A study of a triclad flatworm which lives in the estuaries of streams and is subject to the alternate effects of pure sea-water and pure freshwater. The chemical and physical conditions are described, together with the methods used for the determination of the various factors. With these data a section of the stream conditions from upper to lower was obtained, and the fauna is listed for different stations in this gradient. The times of immersion in different chemical contents of water were noted.

12. Weil, E. and **Pantin, C. F. A.** "The Adaptation of *Gunda ulvae* to Salinity. 2. The Water Exchange." *Journ. Exp. Biol.* **8**, 73–81. 1931.

It was shown by experiment that pure water killed the worms in 48 hours, but that water with a certain amount of calcium carbonate prevented them from swelling up so much. It is suggested that calcium salts control the permeability of the cells. Other substances investigated did not have this effect on *Gunda*. It is therefore probable that *Gunda* is able to survive the low-tide periods in the stream owing to the presence of calcium in the water.

13. Rees, G. "Some Observations on the Biology of Larval Trematodes." *Parasitology*, **23**, 428–40. 1931.

Contains interesting experimental observations on the periodicity of emergence of the cercariae of three species of flatworms which parasitise snails in their first stages. *Cercaria limbifera* (coming from *Limnaea palustris*) showed emergence of the free-living larvae during the day only. When

snails were kept in total darkness emergence was inhibited at first and then continued diurnally as before. The larvae were positively phototropic. *Cercaria* "Z" (from *L. peregra*) also had diurnal emergence, but when placed in the dark the snails produced worm larvae both by day and night. The larvae of this species were negatively phototropic. They showed two maximum times of emergence in the day. As many as 500–1200 came from one snail during 12 hours. *Cercaria cambrensis* (from *Limnaea truncatula*) emerges for its free-living stage both by day and night, but more abundantly at night. Temperature effects, duration of free life of the larvae, and effects on snail hosts, are also described.

14. Thorpe, W. H. "Experiments upon Respiration in the Larvae of Certain Parasitic Hymenoptera." *Proc. Roy. Soc.* B, **109**, 450–71. 1932.

The work was aimed primarily at finding out the function of certain organs in the larvae. The paper includes a valuable account of the use of biological indicators (particularly certain flagellate Protozoa and species of Bacteria) which show migratory movements when the oxygen tension of the water is at a certain optimum level below normal.

15. Fraenkel, G. "Die Mechanik der Orienterung der Tiere im Raum." *Biol. Reviews*, **6**, 36–87. 1931.

(Full summary in English.) An elaborate classification and discussion of the directional movements of animals. Contains a critique of Loeb's theory of forced tropisms, with which the author is not in agreement. A full and valuable bibliography.

16. Belehredek, J. "Temperature coefficients in Biology." *Biol. Reviews*, **5**, 30–58, 1930.

Simple chemical formulae for temperature coefficients are not successful in biology, owing to the greater complexity of the systems studied. It is suggested that diffusion and viscosity are the main limiting factors in biological reactions, and therefore that temperature coefficients in biology are an index of these factors.

17. Atkins, W. R. G. and **Poole, H. H.** "Methods for the Photo-electric and Photochemical Measurement of Daylight." *Biol. Reviews*, **5**, 91–113. 1930.

4. PARASITES OF ANIMALS.

See also **9, 13, 24, 25, 31.**

18. Elton, C., Ford, E. B., Baker, J. R. and **Gardner, A. D.** "The Health and Parasites of a Wild Mouse Population." *Proc. Zool. Soc. London*, 657–721. 1931.

A study of the numbers, reproduction, parasites, diseases, and general ecology of *Apodemus sylvaticus* near Oxford, covering two and a half years field work. Mortality and probable migration of the wood mice were noted in the spring of 1927, at a period for which periodic mortality in wild voles and mice in England had been predicted. The cause of the mortality was not ascertained. A complete ecological survey of parasites (including Protozoa, some Bacteria and *Spirochaeta*) was made, with reference to changes in numbers and age distribution in hosts. Parallel, but less thorough studies were made of *Evotomys glareolus*, *Microtus hirtus*, and shrews (*Sorex araneus* and *minutus*). Great differences from year to year were found in numbers both of hosts and parasites, and these were related to reproduction and mortality and to age distribution of the population.

19. Harper, W. F. "On the Structure and Life Histories of British Freshwater Furcocercariae." *Parasitology*, **23**, 310–24.

A study of several species which pass alternately through snails and waterfowl (material from Morton Loch, North Fifeshire).

20. Smith, K. M. "Virus Diseases of Plants and their Relationship to Insect Vectors." *Biol. Reviews*, **6**, 302–44. 1931.

A complete review of knowledge to date. Many insects act as carriers of virus diseases, but aphids are the most important. One species, *Myzus persicae*, has been found capable of carrying fourteen different viruses. Valuable bibliography.

5. PLANT-GALLS.

21. Barnes, H. F. "Further Results of an Investigation into the Resistance of Basket Willows to Button Gall Formation." *Ann. Applied Biol.* **18**, 75–82. 1931.

Experiments showed that certain species of willow (*Salix purpurea, S. viminalis*, their hybrids, and *S. alba* var. *vitellina*) were immune to the larvae of the gall midge *Rhabdophaga heterobia*. Twelve varieties of *Salix triandra* were very susceptible. A similar type of host specificity in willow beetles has been described. It is suggested that hybrids between the *S. triandra* and the other species might be relatively immune, if they could be produced.

6. FOOD HABITS.

See also **34**.

22. Savage, R. E. "The Relation between the Feeding of the Herring off the East Coast of England and the Plankton of the Surrounding Waters." *Ministry of Agr. and Fish. Fishery Investigations*, Ser. 2, **12**, No. 3, 1–88. 1931. (H.M. Stationery Office. 4*s*. net.)

Following earlier work by Hardy on food of the herring, nearly 14,000 herring stomachs were examined, food species being recorded quantitatively and compared with some 1000 plankton samples from the same area at the same time. Conclusions (backed by careful and elaborate analysis of figures and description of field and laboratory methods) are that the herring has a very wide range of food which depends on the abundance and availability of different species in the plankton, and that there is little evidence of selection. The plankton itself is liable to much variability in place and time, owing to the fluctuating influence of Atlantic currents, which partly serve to renew the organisms eaten by the fish. The effects of this plankton variability on growth and breeding of the fish are discussed. An estimate is made of the amount of plankton eaten by herring at one meal. It is suggested that the total number of herring landed in 1929 (some thousand million, weighing about 150,000 tons), would consume about 300 tons of plankton (dry weight) at one meal.

23. Gray, J. and **Setna, S. B.** "The Growth of Fish. 4. The Effects of Food Supply on the Scales of *Salmo irrideus*." *Journ. Exp. Biol.* **8**, 55–62. 1931.

These experiments on the rainbow trout showed that growth of rings on the scales was influenced by food supply, confirming the assumptions made in field work, in which the narrow rings are taken to represent winter growth on low food supply. No scale periodicity was shown by fish fed fully throughout the year, while fish fed on scanty food had narrower rings than those fed on abundant food.

24. Bristowe, W. S. "Notes on the Biology of Spiders. 5. *Theridion ovatum* Clerck, its Habits and Varieties." *Ann. and Mag. Nat. Hist.* **8**, 466–9. 1931.

Common species making webs on bramble and other plants; ichneumon bred from eggs, phorid fly breeding in dead spiders, nematode worm parasite, and species of preys (flies, bees).

25. Bristowe, W. S. "Notes on the Biology of Spiders. 7. Flies that Triumph over Spiders." *Ann. and Mag. Nat. Hist.* **8**, 471–4. 1931.

Scatophaga stercoraria and wasps steal preys from spider webs; certain flies sit on backs of spiders and sometimes share their prey; summary of data on parasitization of spiders by acrocerid flies, and notes on flies that eat spiders.

26. Hobby, B. M. "A List of the Prey of Dung-flies (Diptera, Cordyluridae)." *Trans. Ent. Soc. South England*, **7**, 35–39. 1931.

Summary of large number of observations of prey of species of *Scatophaga*, based on material in the Hope Department, Oxford, and on the author's observations. Species of prey, date and locality are given in many instances.

27. Hobby, B. M. "The British Species of Asilidae (Diptera) and their Prey." *Trans. Ent. Soc. South England*, **1930**, 1–42. 1931.

Valuable summary of data (mainly unpublished records based on collections accumulated in the Hope Department, Oxford) for 22 species of asilid flies. Diptera are the most common preys, also sawflies and parasitic Hymenoptera. Continental records are included in the summary.

28. Thorpe, W. H. "Further Observations on Biological Races in *Hyponomeuta padella* L." *Journ. Linn. Soc.* **37**, 489–92. 1931.

There are two main biological races: on apple, and on hawthorn or blackthorn. Late larvae or pupae were transferred to different host plants and the egg-laying choice of the adult moths observed under controlled conditions. Moths bred on blackthorn showed a strong but not complete (about 3 : 1) preference for blackthorn rather than hawthorn. In another experiment moths from blackthorn showed about equal choice of the two species, but would not lay at all on cherry. *H. cognatella* does not show the same tendency for formation of biological races. Conclusive results require larger figures and more experiments.

29. Krogh, A. "Dissolved Substances as Food of Aquatic Organisms." *Biol. Reviews*, **6**, 412–42. 1931.

The theory of Pütter that many aquatic organisms feed on dissolved organic matter as well as on solid food is reviewed, and the author concludes that although such dissolved substances do really exist (e.g. 10 mg. per litre were found in Lake Furesö), there is little or no evidence that any animals except certain Protozoa actually use it for food, and that if any do they absorb it through the gut and not the general body surface.

7. THE NUMBERS OF ANIMALS.

See also **4, 17, 18, 22.**

30. Harrisson, T. H. and **Moy-Thomas, J. A.** "St Kilda House Mouse." *Nature*, **129**, 131. 1932.

Has become extremely rare since evacuation of the St Kilda islanders in 1930. An apparently similar species has also been recorded from North Uist, so that St Kilda may be only one of several stations.

31. Elton, C. "The Study of Epidemic Diseases among Wild Animals." *Journ. Hygiene*, **31**, 435–56. 1931.

Many wild animals are subject to periodic epidemics, which are often associated with violent fluctuations in numbers of the population. These occur in insects, crustacea, fish and birds, but are particularly common in wild mammals. A summary of part of the existing published information on the subject is given, and it is pointed out that some mammal fluctuations are sufficiently regular to make forecasting a practical aid to the study of their epidemics. Special summaries are given of cycles in British voles, Norwegian lemmings and voles, Canadian lemmings and foxes, and Bavarian voles. An appendix contains some new records (from various observers) of epidemics in hippopotami, red-backed voles, hares and moles.

32. Harrisson, T. H. "St Kilda in 1931." *Bull. British Ornith. Club*, **154**, 32–36. 1931.

Summary of the ornithological results obtained by a party of scientists who carried out a biological survey in the summer of 1931. Average density of land birds on the main island was one to every 3·75 acres. Rock pipits had unusual local habitat, nesting inland in places normally occupied by meadow pipit. Notes on numbers of other birds, and on probable changes resulting from evacuation of the island in 1930.

33. Harrisson, T. H. "The Birds of the Harrow District (North-West Middlesex) 1925–30." *London Nat.* 82–120. 1930. (Separately reprinted 1931, the School Bookshop, Harrow-on-the-Hill, 1*s.* 6*d.*)

A review of the abundance and distribution of each species, together with many notes on changes in population. At least 27 nesting species have increased in density while decrease has been noted for seven species. The increase is thought by the author to be apparent and not real, and due to greater concentration of birds in areas of land still left free from building which is progressively covering the district. General habitats dealt with include water, sewage farms, oak-hazel woods, birch commons, farm lands and other open spaces. Evidence is given for a concentration of migrant birds in the eastern part of the district, possibly forming part of a localised flight line up the Thames Valley or from the Sussex coast through the Brent, Cambridge, and the Wash. Special discussions of the numbers of some species are given. The density of rooks is given as 2·3 birds per square mile, or about 6·5 per square mile of available feeding ground (i.e. eliminating woods and built-over areas).

34. Tucker, B. W. "The Heron (*Ardea cinerea*) in Somerset. Supplement to Part 1; and Part 2." *Proc. Somersetshire Arch. and Nat. Hist. Soc.* **76**, 31–52. 1930.

The Supplement contains additional census data for 1930. The main paper contains a discussion of the ecological conclusions to be drawn from the census data. The feeding grounds have been roughly mapped out for some heronries in Somerset and it is shown that the heronries are near the feeding areas, with an average range of about 5 miles. Considerable data on food show that eels, frogs and water-voles are commonly eaten. The importance of the latter food is emphasized. A map of the distribution of heronries shows a close relation to the alluvial areas in river valleys. A large number of species of trees are used. Breeding, relation to rookeries, and to predatory birds, and destruction by man are discussed. The number of breeding herons in Somerset is probably about 440 (1930), i.e. one pair to 3759 acres.

35. Southgate, B. A., Pentelow, F. T. K. and **Bassindale, R.** "Death of Fish in the Tees Estuary." *Nature*, **129**, 129–30. 1932.

Great mortality in smolts of salmon and salmon-trout during migration in April–June was found to be probably due to cyanide derived from effluents of coke factories using direct process of ammonia recovery. Oxygen deficiency, and poisons other than cyanide were found insufficient to account for deaths.

36. Orion, J. H. and **Lewis, H. M.** "On the Effect of the Severe Winter of 1928–9 on the Oyster Drills...of the Blackwater Estuary." *Journ. Marine Biol. Ass.* **17**, 301–13. 1931.

Urosalpinx cinerea is an American oyster drill which is apparently replacing the two British species *Murex erinaceus* and *Purpura lapillus* as a dominant oyster pest. (The American slipper limpet *Crepidula fornicata* has also increased in recent years since its introduction.) The winter of 1928–9 was very cold (full temperature data for the sea water for 5 years are given), and apparently destroyed many *Murex* and *Purpura*, while *Urosalpinx* was still abundant in 1929 and 1930. It also destroyed large numbers of the echinoderm *Echinus miliaris*, which suffered in the same way in this Essex area after the cold winter of 1916–17. Of 8000 specimens of the three tingles or drills, taken in 1930, 84 per cent. consisted of *Urosalpinx*.

37. Stephen, A. C. "Notes on the Biology of Certain Lamellibranchs on the Scottish Coast." *Journ. Marine Biol. Ass.* **17**, 277–300. 1931.

Studies of the age distribution and seasonal breeding activity of three bivalves, *Cardium edule*, *Tellina tenuis*, and *Macoma baltica*.

8. MIGRATION AND DISPERSAL.

See also **14, 15, 32, 36.**

38. Pringle, J. W. S. "Butterflies and Moths." *Rept. Winchester College Nat. Hist. Soc.* **1927–31**, 18–20. 1931.

Records changes in abundance, and migration years, of certain species. The comma butterfly, rare until 1929, increased during 1930 but became uncommon again in 1931.

39. Dawe, F. S. "The Comma Butterfly in England." *Nature*, **128**, 760. 1931.

Comments on spread of this species to London. Additional note (*Nature*, **128**, 760–1, 1931) by N. D. Riley, summarises the recent spread eastwards. Further notes for south-west England are given by F. Tutin (*Nature*, **128**, 1041, 1931); there is some evidence that the species has become double-brooded and extended its range of food plants.

REVIEWS

Chapman, Royal N. *Animal Ecology with Especial Reference to Insects.* Pp. x + 464; 153 text-figures, with Appendix by V. Volterra. Price £1. 4*s*. 0*d*. McGraw Hill, London and New York. 1931.

Zoologists, especially entomologists, will be very gratified to have this definitive edition of Prof. Chapman's work, which has for some time been circulating in a mimeographed form. The first half of the book deals with the measurement of the edaphic factors in the environment and with the ways in which they affect animals under controlled conditions. The second half treats of the main types of terrestrial and freshwater communities, of their edaphic peculiarities and of the action of these factors upon the fauna. The treatment is throughout strictly quantitative, the logical outcome of this viewpoint being to aim at reducing all associations to equations involving only matter and energy. With so austere an ideal it is scarcely practicable, with our present knowledge, to take much account of the influence of animals on one another. The work of naturalists has to await re-estimation on a quantitative basis. Chap. viii, however, falling between the two main topics, discusses "Biotic factors in Autecology." Here Prof. Chapman analyses his concepts of "Biotic potential" and "Environmental resistance." The former may be described as the mean power of the species to multiply when all factors, both intrinsic and extrinsic, are taken into account. It is suggested that each species possesses an inherent biotic potential as characteristic of it as a particular valency is of a chemical element. It will not be long before the progress of the quantitative ecologists along these lines forces them seriously to consider those difficulties in defining species which have long confronted the taxonomists. The environmental resistance is measured by the difference between the number of individuals of a species which might be expected from a knowledge of the biotic potential and the number actually found. Ecologists are well aware of the extremely complex interrelations which together determine the environmental resistance but they have hardly begun to devise methods for its quantitative estimation. As Prof. Chapman says (p. 195), "It will not be possible or practical to review the attempts to express the effects of the environment in diminishing the potential number of organisms in an environment. It is still too early in the history of these attempts to be able to select the most promising methods." At the present time the concept appears to have considerable value in suggesting one method of approach to quantitative field ecology. It may be possible to estimate both the biotic potential of a species and the size of the population actually occurring; from these the environmental resistance may be deduced without any detailed knowledge of the individual resistances (climate, parasites, predators, etc.), of which it is the sum. It will probably be found far easier to calculate the biotic potential of warm-blooded animals than of insects, which respond much more rapidly to local climatic fluctuations. It is interesting to find that the actual example given of a calculated environmental resistance is based on the data of the U.S.A. bird census. The progress of ecology in England will be much quickened by the similar censuses now being undertaken at Oxford and elsewhere.

One aspect of all such quantitative work needs emphasizing. The problem that is being investigated is very largely one of adaptation. In a few species of insects we can now say that the northward range is definitely determined by the influence of temperature on their biotic potential. We are no longer forced to argue vaguely as to a possible adaptation to an environment undefined except by its spatial extension. The recent advances in this direction have been made by the applied biologists but the results of their investigations are bound eventually to filter through to those who write and lecture on evolution.

Within the field that he has delimited, Prof. Chapman's book will be found exceedingly valuable. The methods of measuring edaphic factors and of controlling them for experimental

purposes are clearly described, with a number of useful diagrams and a full bibliography at the end of each chapter. The exposition of the so-called "standard" methods of maintaining a constant humidity would, perhaps, have benefited if some of the difficulties of applying them in practice had been more fully considered. The sections dealing with synecology are based mainly on American data but they will be invaluable as an indication of methods to employ elsewhere. The book is completed by an appendix in which Prof. Volterra's papers on the mathematics of animal multiplication are translated from the Italian by Dr Mary E. Wells. Ecologists have for some time had an uneasy feeling that Prof. Volterra's work might be of great importance to them and this impression is now confirmed. Prof. Volterra's formulae have apparently found confirmation in the investigations of Italian fishery experts and with further development of quantitative methods in terrestrial ecology will doubtless soon have their application elsewhere. The thanks of all English-speaking ecologists are due to Prof. Chapman for enabling them to contend directly with the mathematics in their own language.

O. W. RICHARDS.

The Journal of Ecology and Biocenology. Vol. I, no. 1, pp. 1–152, 1931. Edited by M. L. LEVIEN, W. W. STANTSHINSKY and B. A. KELLEV, in collaboration with an Editorial Board. Moscow and Leningrad.

THE value of this new *Journal* will be apparent to all ecologists, since it will enable them to follow in a central publication the results of Russian research on both plant and animal ecology. There are adequate summaries in English or German at the end of the papers, the text being in Russian. The titles of text-figures are in both Russian and English (or German). The present number contains papers on hydrogen ion concentration of soil in relation to mountain plants, migration routes of the Middle Asiatic flora and fauna, the study of dynamics of ecological associations in terms of the amount of living matter, the nests of ants in Turkestan, the present position of ecology in modern zoology, and quantitative methods for the study of grass associations. There are also reviews and notes (in Russian only). Ecologists will wish every success for the new Russian journal, whose contents will be reviewed in future numbers of the *Journal of Animal Ecology*.

Leopold, Aldo. Report on a Game Survey of the North Central States. *Published by the Sporting Arms and Ammunition Manufacturers' Institute, Madison, Wisconsin*, 1931. Price $1.00.

THE profound influence of the colonisation and development of North America upon the native animal population is well shown by this survey of the past, present, and possible future status of game animals and the factors influencing their numbers. The area surveyed covers eight States south and east of Lake Superior, and the work is a serious attempt to trace the causes of the recent decline in the game population and indicate the methods which must be adopted if a supply of animals to be shot is to be maintained in the future. Owing to the fact that the survey is under the direction of a competent ecologist who is also a forestry expert this book is of equal interest to the scientist and the sportsman, though the latter may be more directly interested in the sequel on Game Management which is shortly to be published.

Quail (or "Bobwhite") have received the most comprehensive investigation, and occupy a large proportion of the book, but many of the facts concerning them will be found to have an equal application to most of the other birds and mammals included in the survey. The pioneer farmers found quail by no means numerous on their arrival in the central states, owing to the sharp demarcation which then existed between forest and prairie; quail need local bush cover for nesting and open (preferably cultivated) land for feeding, and unless the forest has extensive clearings or the prairie plenty of small "woodlots" neither is a good habitat. The advent of the early farmer, partially clearing the forest, planting hedgerows

and tree-belts on the prairie, and growing corn wherever he could, produced ideal conditions for quail and other game. Consequently the period 1880–1900 showed a phenomenal increase in quail. But this early rough farming soon changed to a more intensive and economic cultivation of the land: hedges were rooted up and wire fences replaced them, grazing animals became more common and were allowed free access to the forests and woodlots, while odd bits of waste ground carrying trees and scrub were cleared and farmed. The result of this modern farming practice has therefore been to deprive the quail of cover for nesting, while modern methods of harvesting may also have a pronounced effect upon the amount of grain food available on farms during the autumn and winter. The recent agricultural slump has had the effect of producing rather better conditions for quail in some areas, since many farms have been neglected or abandoned and bush cover is beginning to grow again. The revival of shelter-belt planting also promises to provide new cover for game, while the conservation movement is showing results in the way of providing game refuges, winter feeding, close seasons, etc., both by State legislation and private enterprise.

In dealing with absolute numbers of quail and other animals Leopold finds it difficult to obtain conclusive and accurate data—in common with all ecologists who have attempted census work on wild animal populations. On some farms he has found it possible to get reliable counts of the number of covies of quail, but for the majority it is only possible to obtain estimates by local sportsmen and farmers. The census method most commonly used was that of counting the number of covies flushed by a dog per day on any given area, and assuming a standard number of birds per covey. Variation in the size of covies in different years, and the presence of barren pairs, are shown to be important subjects which require further investigation, especially in relation to saturation density and territory. The highest density reached by quail over an area of any considerable size appears to be about one bird per acre: the reason for such a "saturation point" is not clearly understood and forms one of the many interesting problems raised by the survey. The influence of such factors as disease, cyclic fluctuations, weather, and migratory movements upon the quail population is discussed in so far as the evidence allows, and here again the pressing need for continuous scientific enquiry is obvious and admitted.

The chapter on the Game Cycle is one of the most important in the book. The cyclic fluctuations of rabbits, ruffed grouse, and prairie grouse are now shown to be a fact which must be assimilated by sportsmen and everyone intelligently interested in game conservation. On a thorough knowledge of the causes and working of this "game cycle" hangs the whole future of successful conservation. At present very little is known about its behaviour in the United States beyond the fact that rabbit and grouse populations have violent periodic fluctuations coupled with high mortality from epidemic disease, the average length of the cycle being about 9 years but varying somewhat in different localities. Until the working of the cycle is clearly understood there can be no possibility of a really beneficial scheme for close seasons or limited shooting. Leopold's survey clearly shows the incredible dearth of facts concerning this cycle and the behaviour of game populations in general, and indicates the lines which must be followed if American sportsmen and farmers are to derive the full benefit from the game crop—which is certainly a crop amenable to cultivation and one which should give a substantial return for any outlay expended with this book as a guide. Co-operation between the existing organisations, societies, etc., and particularly the alliance of forestry, can do a great deal towards maintaining a sufficient game population. But it is obvious that organisation and administration must have facts to organise and administrate, and the facts which are wanted can only be obtained by scientific research in a field which is of profound interest to every ecologist. It is to be hoped that the problems exposed by this preliminary survey will receive the attention they deserve.

A. D. M.

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